

Proceedings of the American Academy of Arts and Sciences

VOL. 76, No. 2, P. 25-54—APRIL, 1947

---

LOWER PERMIAN INSECTS FROM OKLAHOMA. PART 1.  
INTRODUCTION AND THE ORDERS MEGASEOPTERA,  
PROTODONATA, AND ODONATA

By FRANK M. CARPENTER



# LOWER PERMIAN INSECTS FROM OKLAHOMA. PART 1.

## INTRODUCTION AND THE ORDERS MEGASECOPTERA, PROTODONATA, AND ODONATA

By FRANK M. CARPENTER

Received August 9, 1946

Presented October 9, 1946

### INTRODUCTION

During the past two decades our knowledge of Permian insects has been greatly increased. This has mainly resulted from the collection and study of several thousand specimens from strata in Kansas, Russia and Australia. The rocks in Kansas, termed the Elmo limestone by Dunbar (1924), are geologically the oldest; they belong to the Wellington formation, which is well within the Lower Permian and not far from its base. The correlation of the Russian and Australian beds is not so certain, but they are probably correctly referred to the Upper Permian. The Elmo beds have accordingly been unique: they have provided us with almost the sole record of an early Permian insect fauna. It has been my hope for many years that another insect-bearing bed of equivalent age would be found, especially one deposited under environmental conditions different from those responsible for the Elmo limestone.

This hope has now been realized. In 1939 Dr. G. O. Raasch sent me about seventy well-preserved insects which he had collected in certain Wellington strata in Noble County, Oklahoma. A study of the specimens convinced me that further exploration of these rocks would add substantially to our knowledge of Permian insects, and I accordingly spent the following summer collecting in the region. In this undertaking I was fortunate in having the aid of Dr. Raasch, who made a careful stratigraphic study of the area, and was able to trace the insect-bearing rocks over an area of about 400 square miles. In about ten weeks we collected more than five thousand well-preserved insects.

Dr. Raasch's detailed account of the Wellington formation in Oklahoma is being published elsewhere, but with his permission I include here a summary of his conclusions on the origin of the insect-bearing rocks and the environment of the biota. The Wellington formation as a whole covers a large area. It was deposited in a great water-filled basin, the Wellington Sea, occupying parts of Oklahoma, Kansas, Nebraska and Colorado. In Pennsylvanian time typically marine waters from the ocean to the

south periodically invaded the basin and this inflow continued until early Wellington time. By mid-Wellington, typically marine conditions had ceased to exist in the basin and the climate of the region had become more arid. Although inflow of marine waters continued periodically, presumably through a restricted connection from the open sea to the southwest, the waters covering the basin were at all times of more than marine salinity. The conditions alternated between those of a great salt lake and of a vast, desiccating mud-pan. This alternation was especially pronounced at the time of deposition of the strata in Noble County which Raasch has termed the Midco member of the Wellington formation. This member is about 255 feet thick and is composed mainly of alternating lumpy, clay-shales and fissile, flaky shales. Included in this series is the insect bed. Varying from about six inches to four and a half feet in thickness, it consists in reality of several layers of fine-grained, compact, argillaceous dolomitic limestone, separated by fissile shale. Three of the limestone layers contain insects, and for convenience of reference they have been designated the *lower*, *middle* and *upper* insect layers. The lower layer shows sedimentational and organic features which suggest that it was laid down close to the shore and that most of its biota was washed into the lake. The matrix and biota of the middle layer, which is highly irregular and characterized by pink partings, were probably transported to the water by violent dust storms. The upper layer is highly argillaceous, and was deposited under strongly saline conditions; insects are rare but they are very well preserved.

Midco Salt Lake was essentially a playa, barren of life except for algae and Conchostraca (Crustacea). There is no evidence that insects, either nymphs or adults, lived in the water of the lake itself. Most insects preserved in the limestone were presumably carried to the water by gales or floods and were therefore not all derived from the local environment. Thus, the aquatic nymphs which are abundant at a few localities (e. g. loc. 15) were almost certainly brought to the lake intermittently by small streams

in a flooded condition. Plants did not grow near the lake; they are sparsely represented in the beds by fragments of leaves or wood, which were also carried to the water by winds and floods.

The foregoing account describes a very different environment from that existing in the vicinity of Insect Hill in Kansas, when the Elmo limestone was formed. According to Dunbar (1924) this bed was deposited in a fresh-water lake or lagoon, derived from an earlier swamp. Plants apparently grew close to the water's edge and although most insects were driven into the water by occasional storms, some lived in the water during their nymphal stages. The Elmo Lake was much smaller than the Mideo and consequently presented less diverse environmental conditions. Nevertheless, the two lakes were only about 140 miles apart and apparently nearly contemporaneous.

The Xiphosura and Conchostraca which Dr. Raasch and I collected in the Mideo beds have already been studied and described by Professor P. E. Raymond (1945, 1946). Three specimens of Xiphosura, found in the lower layer at locality 15, represent two new species of a new genus: *Anacantium carpenteri* Raym. and *A. breve* Raym. The genus belongs to the family Euproöpidae, previously known only from Carboniferous strata. The Conchostraca include seven species, all new and representing three families: Lioestheriidae, with *Lioestheria raaschi* Raym., *Pseudestheria brevis* Raym., *Ps. plicifera* Raym., and *Ps. rugosa* Raym.; Limnadiidae, with *Pemphicyclus laminatus* Raym. and *Palaeolimnadiopsis carpenteri* Raym.; and Leaididae, with *Leaia reflexa* Raym. The occurrence of the Leaididae is especially interesting, since the family has previously been known only from Carboniferous strata. *Pseudestheria plicifera* is also noteworthy, for it is the species which occurs, though very rarely, in the Elmo limestone. Apart from the occurrence of insects, the extraordinary abundance of Conchostraca is the most striking characteristic of the Mideo fauna. Although these Crustacea were probably unable to develop prolifically in the hypersaline water of the Lake, they presumably became well established after cyclical inflow of fresh water, which undoubtedly occurred in the spring of certain years. Subsequent evaporation of much of the water in the Lake would cause a reversion to hypersalinity and result in the death of masses of adult Conchostraca. Their eggs, however, presumably survived through this period and hatched when the water again became habitable.\*

\* This is suggested by Sars' experiments (1896) on

Very little can be said at this time about the Mideo insect fauna. It obviously includes the same orders as that at Elmo, as well as many of the genera and a few species; but it also contains families which are not known from the Elmo limestone and even several which have previously been found only in Carboniferous rocks. This is particularly interesting in view of the Carboniferous affinities of some Mideo Xiphosura and Conchostraca. A satisfactory comparison of the insects of the two beds cannot be made until studies of both faunas have been completed.

Because of the extent of the Mideo insect beds, our collections were made at widely scattered localities in the area. Furthermore, since these localities undoubtedly represent some diversity of environments, record has been kept, by number, of the locality at which each fossil was collected. The approximate site of the localities is given in the accompanying table. Similar record has been kept of the layers of the insect bed in which the specimens were found, the letters L, M, U, indicating the lower, middle and upper layers respectively. The present collection of Mideo insects is presumably by no means representative of the fauna. My original project of making a series of annual trips to the beds, although temporarily halted by the war, will now be carried out until a more extensive collection has been secured.

Before closing these introductory remarks, I wish to acknowledge the aid of the Geological Society of America, which financed in part the 1940 collecting trip with a grant from the Penrose Bequest (Project Grant 335-40). All who are interested in fossil insects are deeply indebted to Dr. Raasch for his discovery of one of the most important insect-bearing beds known; and I, in particular, am indebted to him for his indispensable help as a technical field assistant. I am also obligated to Mr. F. H. Ward, of Ward's Natural Science Establishment, for his part in introducing me to Dr. Raasch's discovery. Finally, both Dr. Raasch and I owe thanks to our friends in Noble County who allowed us to collect without restraint on their property.

The following pages deal with the Mideo insects belonging to the Orders Megaseoptera, Protodonata and Odonata. Other orders will be treated in subsequent papers in this series.

the eggs of Limnadia, which developed normally after resting at least seven years in dried mud. From other observations he concluded that these eggs, in order to be able to develop at all, need to lie dry for several successive years.



- Loc. 1. Sw. corner, Sec. 28, T23N, R1W.  
 Loc. 2. Sw.  $\frac{1}{4}$  of Sw.  $\frac{1}{4}$ , Sec. 20, T23N, R1W.  
 Loc. 3. Nw.  $\frac{1}{4}$  of Nw.  $\frac{1}{4}$ , Sec. 4, T23N, R1W.  
 Loc. 4. Se.  $\frac{1}{4}$  of Ne.  $\frac{1}{4}$ , Sec. 34, T22N, R1W.  
 Loc. 5. Sw.  $\frac{1}{4}$  of Se.  $\frac{1}{4}$ , Sec. 4, & Nw.  $\frac{1}{4}$  of Ne.  $\frac{1}{4}$ , Sec. 9, T23N, R1W.  
 Loc. 6. Sw.  $\frac{1}{4}$  of Sw.  $\frac{1}{4}$ , Sec. 10, T23N, R2W.  
 Loc. 7. Ne.  $\frac{1}{4}$  of Nw.  $\frac{1}{4}$ , Sec. 34, T22N, R1W.  
 Loc. 8. Nw.  $\frac{1}{4}$  of Nw.  $\frac{1}{4}$ , Sec. 34, T22N, R1W.  
 Loc. 9. Roadcut  $\frac{1}{2}$  mile south of Ne. Corner, Sec. 33, T21N, R1W.  
 Loc. 10. Ne.  $\frac{1}{4}$  of Nw.  $\frac{1}{4}$ , Sec. 28, T22N, R1W.  
 Loc. 11. Se.  $\frac{1}{4}$  of Sw.  $\frac{1}{4}$ , Sec. 22, T22N, R1W.  
 Loc. 12. Ne.  $\frac{1}{4}$  of Se.  $\frac{1}{4}$ , Sec. 34, T22N, R1W.  
 Loc. 13. Ne.  $\frac{1}{4}$  of Sw.  $\frac{1}{4}$ , Sec. 13, T23N, R2W.  
 Loc. 14. Sw.  $\frac{1}{4}$  of Ne.  $\frac{1}{4}$ , Sec. 14, T23N, R2W.  
 Loc. 15. Sw.  $\frac{1}{4}$  of Nw.  $\frac{1}{4}$ , Sec. 2, T21N, R1W.  
 Loc. 16. Ne.  $\frac{1}{4}$  of Ne.  $\frac{1}{4}$ , Sec. 33, T22N, R1W.

Table 1. Midco Insect Bed.

1940 Localities by sections, ranges, and townships, in Noble Co., Oklahoma.

### Order MEGASECOPTERA

This order is represented in the Midco collection by eighteen species, which I have assigned to eight genera and five families. The Elmo beds in Kansas, which are also of Wellington age, have so far yielded eleven species referable to five genera and four families. These figures indicate that the order Megasecoptera is more abundantly and diversely represented in the Midco fauna than in the Elmo fauna. They are especially significant since about twice as many specimens of insects have been collected at Elmo as in the Midco beds.

The families present in the Midco member include all those found in the Elmo fauna and in addition the family Bardohymenidae. The occurrence of the latter is of much interest, since it contains species closely related to *Aspidothorax*, from the European Carboniferous. All the Megasecopterous genera known from Elmo are likewise included in the Midco fauna, with the single exception of *Permohymen*. Three new genera are represented in the Midco beds, as well as one genus (*Sylwohymen*) described from the Russian Permian, but not known from Elmo. Four of the eighteen species from Oklahoma are apparently identical with those from Elmo; the others are new.

Some of the new species, especially the Martynoviids, furnish interesting evidence bearing on the interpretation of the wing venation of the Megasecoptera and its phylogenetic importance. It is now apparent that the order was a much larger and diversified group than has previously been supposed, with at least two distinct phylogenetic lines within the order. The evidence for these statements and other conclusions which I have reached will be discussed below, after the description of the fossils.

### Family ELMOIDAE

This interesting family has previously been known only from one species, *Elmoa trisecta* Till., from the Kansas Permian. In the Oklahoma collection there

are six specimens representing two new genera and four new species, in addition to *trisecta*. This material provides us with additional information about the family and requires slight modification of the characteristics previously suggested for the group (Carpenter, 1943). In the new specimens, some of which are splendidly preserved, the stem of R is obviously free from the stem of CuA. This condition undoubtedly existed in *Elmoa*, but the flattening of the convexities and concavities at the base of the wing in the specimens of *Elmoa* presumably caused the apparent fusion of the two stems. All well-preserved specimens of Elmoidae have the stem of R very strongly convex, that of CuP strongly concave. The stem of CuA, which joins CuP only at the very base of the wing, is situated on the steeply inclined membrane between R and CuP. Also in all the new species there are at least three anal veins, instead of two, as in *Elmoa*. This is an especially important characteristic, not elsewhere known among the Megasecoptera.

The outstanding characteristics of the Elmoidae are (1) the independence of the stems of R and CuA, (2) the absence of coalescence between Rs and MA, and (3) the proximal convergence of the strongly convex CuA and R, forming an angle bisected by stem of M. The last characteristic is present also in the Martynoviidae and Asthenohymenidae.

The family Elmoidae, especially as represented by the new genus *Parelmoo*, appears to have a relatively generalized venation and to have several venational features suggestive of the Palaeodictyoptera. Indeed, arguments for placing *Parelmoo* in the Palaeodictyoptera could readily be advanced; but any such assignment would involve not only *Elmoa*, but the Martynoviidae and Asthenohymenidae. Also concerned in this question is the Carboniferous genus *Diaphanoptera*, a detailed account of which is being published elsewhere.<sup>1</sup>

<sup>1</sup> Studies on Carboniferous Insects from Commeny, France. Part II (in preparation).

*Elmoa trisecta* Till.

*Elmoa trisecta* Tillyard, 1937, Amer. Journ. Sci., **33**: 84. Carpenter, 1943, Proc. Amer. Acad., **75**: 56.

There is a single specimen (4736ab) of this in the material from the Midco beds; it was collected at locality 8-M, and consists of the proximal third of a wing. Its venation, as far as known, is identical with that of the Kansan specimens.

**Parelmooa**, new genus

Related to *Elmoa*. Fore wing: Sc terminating on costal margin slightly beyond mid-wing, i. e., just beyond first fork of Rs; Rs arising nearer the base than in *Elmoa*, with three branches, and joined by a cross-vein to MA basally (as in *Elmoa*), but the cross-vein is nearer the origin of MA and further from the origin of Rs than it is in *Elmoa*; MA simple, MP forked; CuA and CuP unbranched; 1A well developed, extending to midwing and with three branches; 2A and 3A present, the latter branched from the base. Cross-veins numerous. Hind wing: Sc closer to R than in the fore wing; anal veins apparently as in fore wing.

Genotype: *Parelmooa revelata*, n. sp.

This genus differs from *Elmoa* chiefly in having a longer Sc and greater development of anal veins.

an individual trait). Cross-veins are numerous but weak, except those at base of costal space. The distribution of preserved cross-veins in the type indicates that others discernible in the specimen were originally present. Hind wing unknown.

Holotype: No. 4822ab, Museum of Comparative Zoology, collected in the Midco insect bed (loc. 15-L), Noble Co., Oklahoma, by F. M. Carpenter and G. O. Raasch. The specimen is a complete and splendidly preserved fore wing.

**Parelmooa radialis**, n. sp.

## Figure 2

Fore wing: length, 15 mm.; width, 5 mm. Shape and venation (as far as known) as in *revelata*, except that R4 + 5 is unbranched, and R2 + 3 divides shortly after its origin. There is a suggestion of a terminal twig on R2, but this is almost certainly an individual trait. Only a few cross-veins are present in the type, outside of the costal space. The anal veins are unknown. Hind wing: length, 12 mm.; width, 4 mm.; costal margin and stem of R straighter basally than in fore wing (as is true of *Elmoa*); venation otherwise like fore wing, including the branching of Rs. 1A and 2A unbranched; 3A

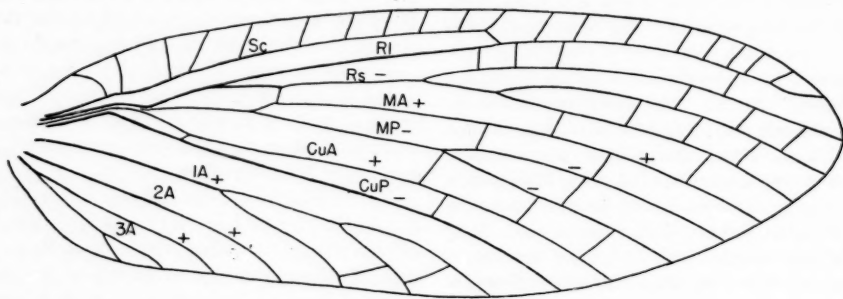


FIGURE 1. *Parelmooa revelata*, n. sp. Drawing of fore wing (holotype). Sc, subcosta (concave); R1, radius (convex); Rs, radial sector (concave); MA, anterior media (convex); MP, posterior media (concave); CuA, anterior cubitus (convex); CuP, posterior cubitus (concave); 1A, 2A, 3A, anal veins.

**Parelmooa revelata**, n. sp.

## Figure 1; plate 2, figure 2

Fore wing: length, 15 mm.; width, 5 mm.; broadest across the middle or not much beyond; Sc connected to R1 by a distal cross-vein; R2 + 3 long, unbranched; R4 + 5 forking slightly after its origin; MP forked at about the level of first fork of Rs; 1A forked at about half its length and again somewhat beyond this; 2A simple; 3A giving rise distally to a posterior branch, which is in turn twigged distally (probably

branched much as in *revelata*. Cross-veins weakly preserved in the type and those of the costal space are not discernible.

Holotype: No. 4825, Museum of Comparative Zoology, collected in the Mideo insect bed (loc. 15-L), Noble Co., Oklahoma, by F. M. Carpenter and G. O. Raasch. This consists of a nearly complete hind wing, moderately well preserved. Paratype: No. 4824, (loc. 8-M), Museum of Comparative Zoology, consisting of a well preserved fore wing, lacking the anal area.

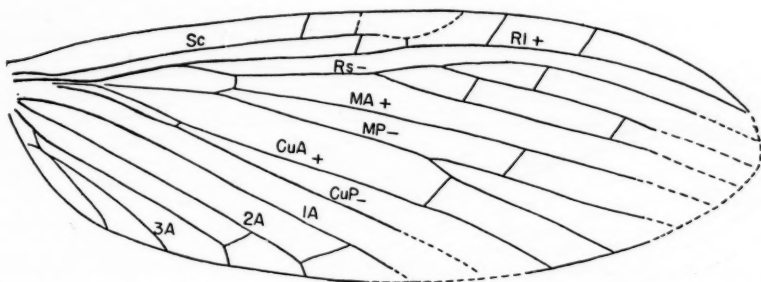


FIGURE 2. *Parelmoa radialis*, n. sp. Drawing of hind wing (holotype). Lettering as in figure 1.

This species is distinguished from *revelata* on the basis of the structure of Rs and 1A. Although the anal veins are lacking in the paratype (fore wing), I have associated this with the holotype (hind wing) because of the similar form of Rs. The difference in branching of Rs in the two species might, of course, be due to individual variation. However, in the seven known specimens of the *Elmoa trisecta* from the Elmoa beds, the branching of Rs is strikingly constant and I assume the same stability for *radialis* and *revelata*. The branching of 1A is also markedly different in *radialis* from what it is in *revelata*, but of course this vein is known only in the hind wing.

***Parelmoa obtusa*, n. sp.**

Figure 3

Fore wing: length, 17 mm.; width, 5.5 mm.; broadest in distal third of the wing; apex broadly rounded; costal margin not so convex as in *revelata* and *radialis*; Sc somewhat longer than in the latter two species; R2 + 3 forked, R4 + 5 unbranched; 1A with a terminal fork; 2A unbranched; 3A with a forked posterior branch. Cross-veins apparently fewer than in *revelata*, many arranged obliquely. Hind wing unknown.

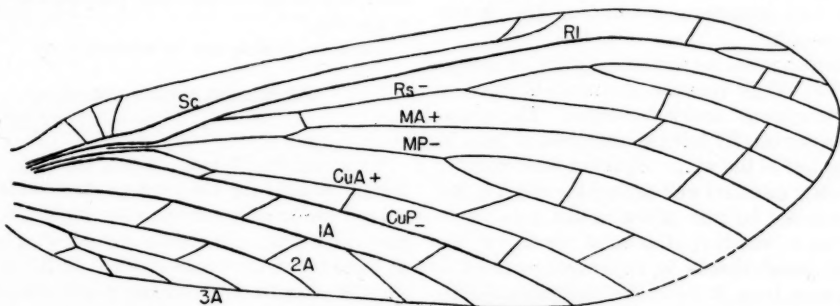


FIGURE 3. *Parelmoa obtusa*, n. sp. Drawing of fore wing (holotype). Lettering as in figure 1.

Holotype: No. 4823 ab, Museum of Comparative Zoology; collected in Midco insect bed (loc. 15-L), Noble Co., Oklahoma, by F. M. Carpenter and G. O. Raasch. This is a complete and well preserved fore wing.

***Pseudelmoa*, new genus**

Related to *Parelmoa*. Fore wing: Sc extending far beyond level of first branch of Rs; Rs with at least five terminal branches; Rs arising further proximad than in *Parelmoa*; MP forked; three anal veins, 1A long, extending to about mid-wing; cross-veins about as numerous as in *Parelmoa*. Hind wing unknown.

Genotype: *Pseudelmoa ampla*, n. sp.

This genus is notable for the length of Sc and the numerous branches of Rs.

***Pseudelmoa ampla*, n. sp.**

Figure 4

Fore wing: length (as preserved), 20 mm.; width, 6 mm.; estimated length, 22 mm.; costal margin not convex; Sc terminating beyond fork of R2 + 3; MA apparently arising near mid-wing but a weak and probably adventitious vein at this point makes the origin uncertain; 1A with a distal fork; cross-

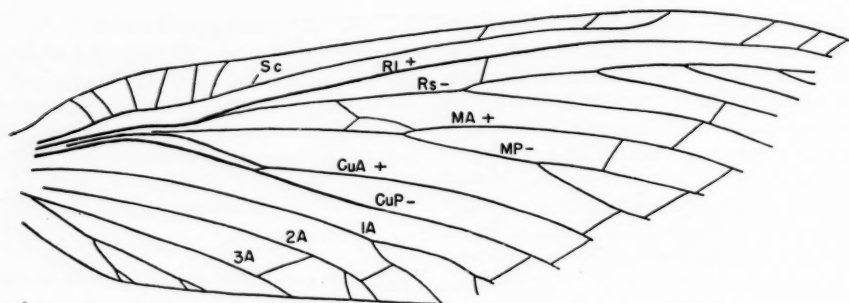


FIGURE 4. *Pseudelmoa ampla*, n. sp. Drawing of fore wing (holotype). Lettering as in figure 1.

veins as shown in figure though probably not all are discernible. Hind wing unknown.

Holotype: No. 2826ab, Museum of Comparative Zoology, collected in the Midco insect bed (loc. 15-L), Noble Co., Oklahoma, by F. M. Carpenter and G. O. Raasch. This consists of a well preserved fore wing, lacking the distal portion.

#### Family BARDOHYMENIDAE

This family was erected by Zalesky (1937) for *Bardohymen magnipennifer* from the Permian of Russia. Since the unique specimen representing that species consisted of the distal half of the wing only, the family could not be satisfactorily defined. The collection from Oklahoma contains a complete wing of a species (*Calohymen permianus*, n. sp.) obviously closely related to *Bardohymen*. The family is therefore redefined here with the aid of the information now at hand. We do not, of course, know for certain that the proximal half of the wing of *magnipennifer* is like that of the new species; should it turn out to be very different, a new family will be needed for *Calohymen*. In the Midco collection there is also an incomplete wing of a species apparently belonging to the genus *Sylwohymen*, which was described by Martynov from the Russian Permian and tentatively referred to the family Bardohymenidae.

The Bardohymenidae were larger than the Protohymenidae. Their venation was much like that of the Carboniferous Aspidothoracidae. The costal space was narrow, R1 being submarginal, at least in the distal half of the wing. Sc is not clear distally; it apparently extended well beyond the origin of Rs, which arose not far from mid-wing and gave rise to at least three branches; M arose at the base of the wing and though close to R, apparently retained its independence from R (as in the Aspidothoracidae) and diverged away from R well before the origin of Rs; MA was not anastomosed with Rs; Cu was ap-

parently anastomosed with the stem of M for a short interval; CuA was not anastomosed with M or MP; a single anal vein was present, formed as in *Aspidothorax*; cross-veins were numerous but there were not more than twenty-five in all. The differences between the fore and hind wings have not been determined; probably the wings were nearly homonomous, as in *Aspidothorax* and most other Megaseoptera.

The closest relatives of this interesting family are the Aspidothoracidae from the Carboniferous of Commeny. Zalesky placed Bardohymenidae in the Suborder Protohymenoptera, presumably because of the proximity of Sc and R1 to the margin; but the family has much more in common with the Aspidothoracidae than with Protohymenidae or its relatives. This is one of the several examples, noted in this paper, of the occurrence of Carboniferous types in the Midco fauna.

#### *Calohymen*, new genus

Related to *Bardohymen*. Sc apparently terminating beyond mid-wing; R1 not forked distally; Rs with three branches; MA, MP, CuA and CuP unbranched; two distinct rows of cross-veins, even the outer row being remote from the posterior margin of the wing.

Genotype: *Calohymen permianus*, n. sp.

#### *Calohymen permianus*, n. sp.

##### Figure 5

Wing: length, 25 mm.; width, 6.5 mm. Costal margin straight for the proximal two-thirds of the wing, then broadly curved; apex slightly rounded; posterior margin only slightly curved; wing broadest at the level of the origin of R4 + 5; R1 diverging slightly away from the margin above the branches of Rs, connected to the margin by two cross-veins (at least in type); no pterostigmal thickening visible;

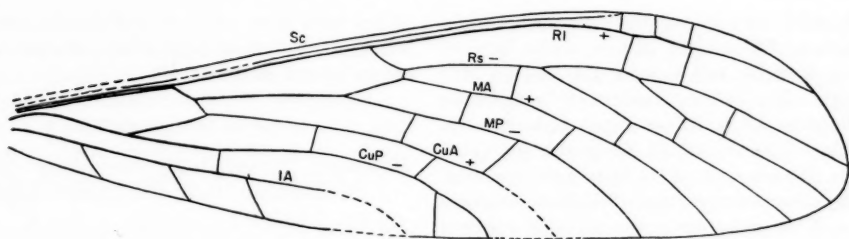


FIGURE 5. *Calohymen permianus*, n. sp. Drawing of holotype. Lettering as in figure 1.

Rs arising slightly before mid-wing; R4 + 5 only a little longer than R3; two long cross-veins between Rs and R1; MA arising slightly proximad of the origin of Rs, connected to Rs by a short cross-vein; CuA arising well before the divergence of M from R1 and connected to M by an oblique cross-vein; CuP has a slight terminal branch, which is probably formed by an oblique cross-vein (as in *Aspidothorax*); IA with four veinlets leading to the hind margin; between all main veins (except CuP and IA) there are two cross-veins arranged as shown in figure 5.

Holotype: 4687ab, Museum of Comparative Zoology; collected in Midco insect beds (loc. 15-L), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). It consists of a well preserved wing, complete except for a small piece along the posterior margin at the end of CuA.

This species is of much interest because of its resemblance to *Aspidothorax*, a drawing of which is included here (figure 6).<sup>2</sup> Unlike the condition in *Protohymenidae*, etc., MA is free from Rs and CuA is free from M. So close is *Calohymen* (and presumably *Bardohymen*) to *Aspidothorax* that it is difficult to find many differences between the two. Sc is possibly slightly longer in *Aspidothorax* than in *Calohymen*; MP is deeply forked in *Aspidothorax* but

<sup>2</sup> An account of the structure and relationships of *Aspidothorax* is included in my revisional study of *Commentry* insects, Part II, now in preparation.

simple in *Calohymen*; and the number of cross-veins in *Aspidothorax* is approximately twice that in *Calohymen*. These differences are probably sufficient to justify the retention of the family *Bardohymenidae*, but they are much less than have previously been found between Permian and Carboniferous Megasecoptera.

#### Genus *Sylvohymen* Martynov

*Sylvohymen* Martynov, 1940, Trav. Inst. Paleont. 11: 10.

This genus was based on a distal fragment of a wing (*robustus*) and placed by Martynov in the family *Bardohymenidae*, although its relationships will not be certain until more of the wing is known. In the Midco collection there is a distal fragment of a wing which resembles that of *robustus* to a remarkable degree. I therefore place the species in *Sylvohymen* until more of its structure is known.

#### *Sylvohymen ingens*, n. sp.

##### Figure 7

Wing: length of fragment, 18 mm.; width, 9 mm.; estimated length of complete wing, 50 mm. Costal margin thickened distally, as far inward as R1; R1 diverging away from the margin only very slightly near the apex, with three short cross-veins between it and the margin; Rs with 4 branches, R2a, R2b, R3, and R4 + 5; a long cross-vein between R1 and

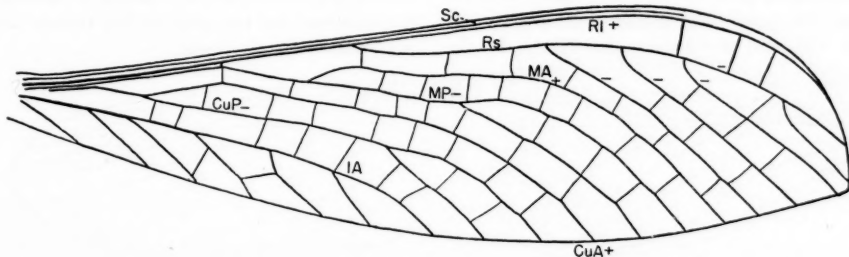


FIGURE 6. *Aspidothorax* sp. (Carboniferous of Commentry, France). Original drawing of fore wing, based on specimens in the Muséum National d'Histoire Naturelle, Paris. Lettering as in figure 1.



the fork of R2 + 3 and a shorter cross-vein near the apex between R1 and R2; one cross-vein between each branch of Rs; two between R4 + 5 and MA.

Holotype: No. 4673ab Museum of Comparative Zoology; collected in Mideco insect beds (loc. 3), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This consists of the distal part of a wing. Since the preserved part does not include the origin of R4 + 5, it probably represents only about a third of the entire wing. This species was apparently only a little larger than *robustus*, which Martynov estimated to have a wing length of 40 mm.

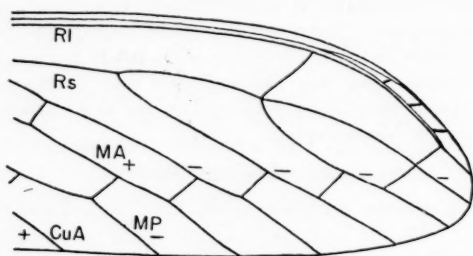


FIGURE 7. *Sylbohymen ingens*, n. sp. Drawing of holotype. Lettering as in figure 1.

The similarity between the venation of *robustus* and that of *ingens* is very striking, though of course the proximal parts of the wings may not have been so much alike. As Martynov points out, *Sylbohymen* (as far as known) is closer to *Bardohymen* than it is to any other Megasecoptera. Additional and more nearly complete specimens will be needed to make certain of this; if it should turn out that Rs is anastomosed with MA, as it is restored in Martynov's figure, the systematic position of the genus will be very different.

#### FAMILY MARTYNOVIIDAE

This family has previously been known from the lower Permian of Kansas (Elmo), where it is represented by the genus *Martynovia*, with two species (*insignis* Till. and *protohymenoides* Till.). In the

Mideco beds there are four new species, described below; one of these belongs to *Martynovia*, the others to new genera.

#### Genus *Martynovia* Till.

*Martynovia* Tillyard, 1932, Amer. Journ. Sci., **23**: 13; Carpenter, 1943, Proc. Amer. Acad. Arts Sci., **75**: 58.

In my discussion of this genus (1943), I stated that the radial sector included from 3 to 5 branches; since the number of branches of Rs in the new species is seven, the definition of the genus is now altered to that extent. In all other respects (so far as known) the following species conforms to the generic definition.

#### *Martynovia longipennis*, n. sp.

##### Figure 8

Fore wing: length, 20 mm.; width, 4.5 mm. Costal margin slightly concave basally, but with a distinct bulge above origin of MA; rest of margin with slight convexity; posterior margin smoothly convex; base of wing more narrowed than in *protohymenoides*; apex of wing unknown; at least two prominent cross-veins in costal space, at the level or origin of CuP; Sc weak distally, terminating at about mid-wing; R1 also very weak apically; both Sc and R1 apparently end in a faint pterostigma, as in *M. protohymenoides*; 4 or 5 well developed cross-veins between Rs and R1; Rs with seven branches, although this number is probably slightly variable in individuals; MA anastomosed for a short distance with Rs, much as in *insignis*; M arising from the stem of R in the manner characteristic of the genus, i. e., at the point of divergence of CuA from the same stem; CuP and 1A are like those of *protohymenoides*, but 2A is very short, having almost been lost by the narrowing of the base of the wing; two cross-veins present between MA, MP, CuP, and 1A, and probably two also between the branches of Rs, though they are not preserved in the fossil.

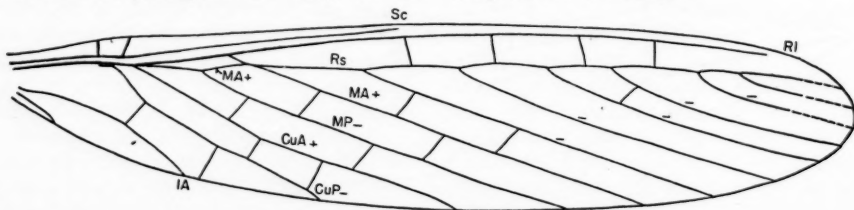


FIGURE 8. *Martynovia longipennis* n. sp. Drawing of fore wing (holotype). Lettering as in figure 1.

Hind wing unknown.

Holotype: No. 4676, Museum of Comparative Zoology; collected in the Midco insect beds (loc. 16), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This is a well preserved wing, complete except for the very apex. The narrowness of the wing, especially basally, indicates that it is a fore wing.

Although this species has much longer wings than the genotype (*insignis*), its venation is essentially the same as that of the latter. In wing shape *longipennis* is similar to *protophymenoides*, but the greater number of branches of Rs and the very short 1A are obvious differences. The pterostigma of *longipennis* is not indicated by coloration; but the faintness of Sc and R1 distally shows that the pterostigma was present and formed essentially as in *protophymenoides*.

#### *Eumartynovia*, new genus

Fore wing: long and moderately slender. Costal space of normal width basally, but narrowed above end of Sc, at which point there is a pronounced bend in the margin of the wing; Rs arising almost at mid-wing and giving rise to four branches; M arising from the stem of R + M at the point of origin of CuA, as in *Martynovia*; MA anastomosed with Rs and also with R, well before the origin of Rs; MA, MP, CuA, CuP, and the anals all unbranched; cross-veins few in number. Pterostigma very long and colored, but not very thick.

Hind wing unknown.

Genotype: *Eumartynovia raaschi*, n. sp.

This genus, although close to *Martynovia*, is distinguished chiefly by having the costal margin distinctly indented at about mid-wing, and by having MA coalesced with the radius well before the origin of Rs.

#### *Eumartynovia raaschi*, new species

Figure 9; plate 2, figure 1

Fore wing: length, 22 mm.; width, 5 mm. Costal margin smoothly arched from the base to about the

middle of the wing; unevenly arched from mid-wing to apex; apex pointed; posterior margin smoothly curved; three pterostigmal cross-veins in costal area, two of them near the level of the origin of CuP, the other near the end of Sc; Sc ending at about mid-wing, slightly beyond the level of the origin of Rs; a heavily pigmented pterostigma extends from the end of Sc to slightly beyond the apex of the wing; this is confined to a narrow strip for most of its length, but near the fork of R2, it extends medially as far as R2 and R2a; between Rs and R1 there are three long cross-veins, and between the branches of Rs, as well as between MA, MP, CuA, CuP, and 1A there are two cross-veins; the free basal piece of MA is short, MA anastomosing with R1 so that R + MA is nearly equal in length to MA + Rs; 1A well developed, 2A short.

Holotype: No. 4680ab, Museum of Comparative Zoology; collected in the Midco beds (loc. 15-L), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This species is named for Gilbert O. Raasch, who was first to find insects in the Midco strata. The holotype specimen is a strikingly preserved fore wing (plate 2, fig. 1).

This insect is remarkable for the long pigmented pterostigmal area. The species of *Martynovia* also have a long pterostigma, but so far as known in none of them is it as long or as heavily pigmented as in *raaschi*.

#### *Phaneroneura*, new genus

Allied to *Martynovia*. Fore wing: slender or moderately broad. Costal space of moderate width basally, narrowed at the level of origin of Rs; costal margin straight or nearly so; only one cross-vein apparently present in costal space; Rs arising just before mid-wing, with two or three branches; M arising from the stem of R + M at the point of separation of CuA from R + M, as in *Martynovia*; MA separating from MP very shortly after the origin of M, and anastomosing immediately with R, the free basal piece of MA being very short; R + MA longer than Rs + MA; MA, MP, CuA, CuP

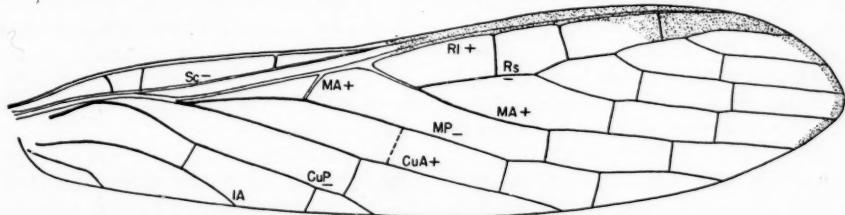


FIGURE 9. *Eumartynovia raaschi* n. sp. Drawing of fore wing (holotype). Lettering as in figure 1.



and anals all unbranched; cross-veins very few; pterostigma apparently formed as in *Martynovia*, unpigmented and weak.

Genotype: *Phaneroneura martynovae*, n. sp.

All the specimens of this genus being isolated wings, we have no knowledge of the differences, if any, between the fore and hind wings. Although some of the wings are slightly broader basally than others, none show the obvious differences in shape exhibited by the fore and hind wings of *Martynovia*.

This genus contains the most highly specialized *Martynoviids* so far known. The outstanding characteristics of the genus are the extensive anastomosis of MA with R, before the origin of Rs; and the reduction in the number of cross-veins and branches of Rs.

***Phaneroneura martynovae*, n. sp.**

Figure 10

Fore wing: length, 12.5 mm.; width, 3 mm. Costal margin nearly straight, with only a slight in-

crease at the base. It may be a hind wing, however, since the posterior margin is slightly more rounded basally, and the origins of M, CuP and CuA are nearer the base than in the holotype. No. 4670, same collecting data (loc. 15-L); this is a nearly complete wing, lacking the proximal fifth of the wing.

In addition to these, there are three more poorly preserved specimens: No. 4739 (loc. 15-L); no. 4740 (loc. 8-M); and no. 4677ab (loc. 15-L). The last specimen consists of the distal half of a wing 3.5 mm. wide; this may be a hind wing.

This species has been named for Olga Martynova, who worked on fossil insects for many years with her husband, Dr. A. B. Martynov, and who has continued her studies independently since his death in 1938.

***Phaneroneura reducta*, n. sp.**

Figure 11

Fore (?) wing: length, 7 mm.; width, 2.5 mm. Costal margin almost straight, as in the genotype;

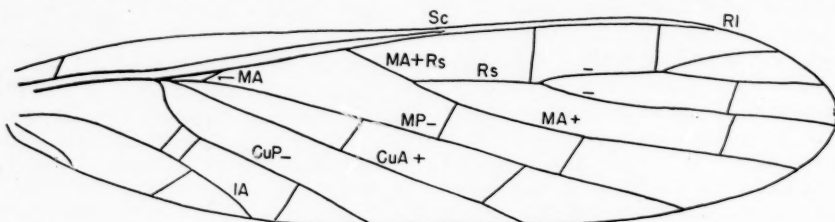


FIGURE 10. *Phaneroneura martynovae* n. sp. Drawing of fore wing based mainly on holotype. Lettering as in figure 1.

dication of concavity; apex narrowly rounded; costal space narrow at base, widest at level of origin of CuA; Sc weak distally, ending about mid-wing; pterostigma indicated only by a slight thickening of membrane; Rs forked twice, forming three branches, a strong cross-vein is present between Rs and R1 at each of these forks; R + M longer than MA + Rs; CuA nearly straight; CuP diverging abruptly away from the stem of Cu; 1A long, curved, 2A very short. Two cross-veins are present between most of main veins and branches of Rs, their arrangement slightly variable in individuals.

Holotype: No. 4675 ab, Museum of Comparative Zoology; collected in Mideo insect beds (loc. 15-L), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This is a well preserved and complete wing.

Paratypes: No. 4738, Museum of Comparative Zoology same collecting data as holotype, except for quarry no. 8-M. This specimen is also a complete wing, with a venation almost identical with that of

apex broadly rounded; posterior margin strongly and evenly curved; costal space relatively broader above origin of CuA than in *martynovae* and more abruptly narrowed at end of Sc; Sc terminating at the middle of the wing; pterostigma very weakly indicated by slight thickening of membrane; Rs with but one fork though in the holotype only there is a weak incomplete vein running from R2 + 3 towards the end of R1; one cross-vein between Rs and R1, at the fork of Rs; MA + R much longer than MA + Rs; CuP not so abruptly diverging from the base of Cu as in *martynovae*, arising from the stem just proximal to the point of separation of MP and CuA (at least in holotype); 1A long; only one cross-vein between the main veins of the wing, and none at all between R2 + 3 and R4 + 5.

Holotype: No. 4733ab, Museum of Comparative Zoology; collected in Mideo insect beds (loc. 15-L), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This specimen consists of an excellently preserved wing, complete except for the very base.

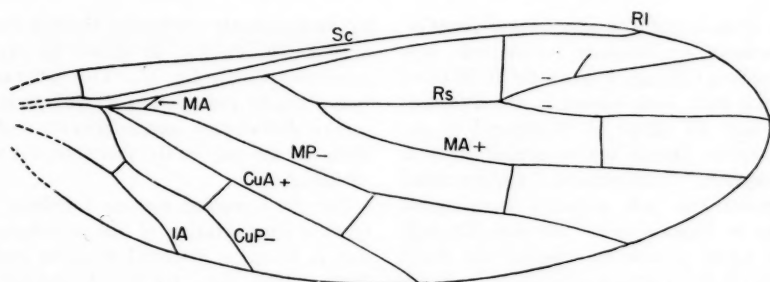


FIGURE 11. *Phaneroneura reducta*, n. sp. Drawing of wing, based mainly on holotype. Lettering as in figure 1.

Paratypes: No. 4737ab, Museum of Comparative Zoology; same collecting data (loc. 15-L); this is also nearly a complete wing, lacking only the very base; its venation is identical with that of the holotype, except for the absence of the adventitious vein from  $R2 + 3$ . No. 4741ab, same data (loc. 15-L); this is a well preserved wing lacking more of the base than the other specimens; it is 6 mm. long and 2.5 mm. wide;  $R2 + 3$  lacks the adventitious vein.

The three specimens on which this species is based may be hind wings and I have considered the possibility that they might represent the hind wing of *martynovae*. However, in none of the other Martynoviidae or in fact in none of the Megasecoptera as a whole so far known, do the fore and hind wings differ in venation, except of course for slight contour of the veins, etc. The specimens of *reducta* are distinctly different in venation from those of *martynovae*: Rs has only one fork instead of two, and there is only one cross-vein between all main veins, instead of two. Furthermore, the wings of *reducta* are only about half the size of those of *martynovae*, a difference which is not known to occur between the fore and hind wings of Megasecoptera. It is my conviction therefore, that even if these specimens are hind wings, they do not belong to *martynovae*.

#### Family Protohymenidae

This family has previously been found in the Permian of Kansas and Russia. In the Oklahoma collection it is represented by four new species and one (*Protohymen readi* Carp.) already described from the Elmo limestone. Before discussing these species, however, I wish to consider certain venational aspects of the Protohymenidae which need clarification. The homologies of the wing veins of the Carboniferous Megasecoptera have been generally agreed upon, for although in some genera there is slight venational anastomosis, the identity of all main veins is obvious. This is also true of the vena-

tion of most Permian genera, in spite of the increased amount of anastomosis; and the interpretation which I proposed (1931) for such specialized genera as *Protohymen* and *Permohymen* has been generally accepted (Tillyard, 1936, p. 447). Martynov, although accepting this view in relation to other views, advocated a very different interpretation of the structure of Rs. He believes that the condition of the radius in *Eohymen* Mart. (1937) and *Aspidohymen* Mart. (1930) represents an early stage in the evolution of this vein, ultimately leading to its structure in the Protohymenidae. In *Aspidohymen*, according to Martynov, Rs divides early into a distal branch (Rsds) and a proximal branch (Rspr); the former arises from the stem of Rs, then anastomoses with R1, only to branch off again distally. In *Eohymen* the anastomosis of Rsds with R1 takes place further proximally, so that it appears to arise directly from R1. The amount of anastomosis of Rsds with R1 has increased during the subsequent evolution of the Protohymenoptera; in *Protohymen*, the origin of Rsds from R1 is at the level of the pterostigma; and in *Asthenohymen* the coalescence is complete. It is on the basis of the coalescence of these veins that Martynov separates the Protohymenoptera from the Order Megasecoptera, in which there has been no such anastomosis.

I have two main objections to this proposal. In the first place, the evidence provided by *Aspidohymen* and *Eohymen* is very questionable. *Aspidohymen* is known by two species, *extensus* Mart. (1930, 1937) and *chopardi* Zal. (1937) from the Russian Permian.<sup>3</sup> Both of these species are based on unique wings, each lacking the proximal third. We have no knowledge, therefore, of the origin of any main veins except Rs. The part of the venation that is known is different in several respects from

<sup>3</sup> Only *extensus* was known to Martynov, *chopardi* having been described just before his death.

that of the Protohymenidae and related families. In both species of *Aspidohymen*, for example, MA is forked (convex),<sup>4</sup> though it is simple in all other families which have been placed in the Protohymenoptera; and Rs (Rspr of Martynov) is unbranched, another feature not occurring in other Protohymenoptera.<sup>5</sup> Furthermore, I am convinced that Martynov has not correctly homologized certain veins in Aspidohymen. He does not indicate in his figure of *extensus* whether the distal branch of Rs (Rsds) is convex or concave; probably its nature was not suggested in the poorly preserved type. But Zalesky's figure of *chopardi*, which is based on a better fossil shows this vein to be convex (+), not concave. It cannot therefore be a branch of the concave Rs.

The genus *Eohymen* is also based on a poorly preserved wing, as indicated by the broken and dotted lines in Martynov's figure (1937, fig. 1). There are many features of the preserved part of the wing which are entirely foreign to the Protohymenidae, etc., such as the double row of cells between certain veins and the remoteness of R from the costal margin. Martynov presents no evidence showing that this wing is actually related to the Protohymenidae, but even if we assume that it is, the gap between it and *Protohymen* is too great for it to be taken as the basis of the explanation of the protohymenid wing.

The Protohymenidae, also, furnish evidence which refutes Martynov's theory of the protohymenopterous venation. A detailed examination of the pterostigmal area of *Protohymen* shows R1 running along the posterior edge of the pterostigma. After giving rise to the vein *a* (figure 12A), it appears to continue for a short distance along the pterostigma (b). A similar condition occurs in all species of the genus, with but slight variation. The pterostigmal area of *Permohymen* is obviously of the same general type. Now Martynov identified the vein *a* as the reduced distal branch of Rs (Rsds),

but he apparently overlooked the fact that this vein is distinctly convex, as shown in my figure of *permianus* (1930, fig. 1). The convexity of this vein is clearly indicated in all well preserved specimens of *Protohymen*, especially in those of the Midco beds. It can only be R1, therefore, not a part of Rs (concave).

For the foregoing reasons I believe that Martynov's interpretation of the protohymenid venation is based on doubtful evidence and has more facts against than for it. A simpler and more direct explanation of the pterostigmal area in the Protohymenidae was contained in my first paper on the Protohymenoptera (1930) but was overlooked by Martynov. The suggestion was made there that the apparent anterior "branch" of R1 (b in figure 12) might be a modified cross-vein. An ob-

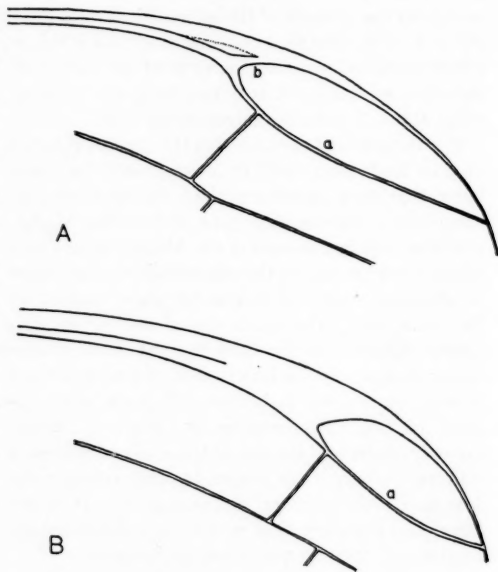


FIGURE 12. Pterostigmal area. *Protohymen venustus*, n. sp. (A); and *Permohymen schucherti* Till. (B), from the Lower Permian of Kansas. For lettering see text.

lique cross-vein actually does occur at this point in many Megasecoptera, though it is usually weakly preserved. A slight change in the angle of inclination of this cross-vein, together with the thickening of the pterostigma, would produce the condition found in *Protohymen*.

#### Genus *Protohymen* Till.

*Protohymen* Tillyard, 1924, Amer. Journ. Sci. (5) 8: 114; Carpenter, 1930, Psyche, 37: 349.

<sup>4</sup> In spite of the convexity of both branches of MA, Martynov identified the anterior one as Rs4.

<sup>5</sup> It should be noted that the nature of the origin of Rs in *Aspidohymen* is uncertain. In his original drawing of *extensus* Martynov showed three thin lines above his Rs (at origin of Rs); in my copy of his figure (1930, fig. 4), I omitted the posterior one of these three, being under the impression that two of the lines represented the width of R. Martynov called attention to this omission (1937, p. 63) and stated that only by omitting that vein would my interpretation be possible. However, Zalesky's later figure of *chopardi* shows no such vein there in his better preserved fossil, his drawing being exactly like my copy of Martynov's in that respect.

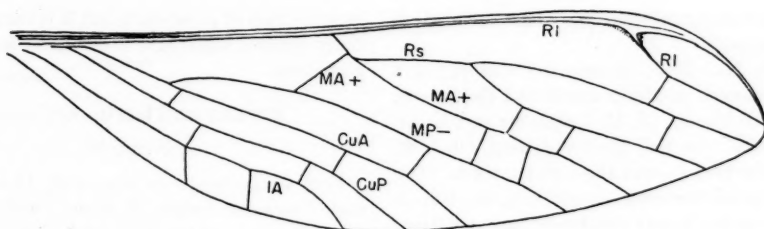


FIGURE 13. *Protohymen curvatus*, n. sp. Drawing of fore wing (holotype). Lettering as in figure 1.

***Protohymen curvatus*, new species**

Figure 13

Fore wing: length, 12 mm.; width 3.5 mm.; wing membrane distinctly uneven, the center of the cells of the wing bulging slightly above the edges. Costal margin straight or nearly so, as far as the middle of pterostigma; apex pointed, the tip of the wing more posterior than anterior; posterior margin strongly curved for its entire length; Sc and R1 as in *permanus*; MA anastomosed with Rs for a very short distance only; IA more remote from the margin than in *permanus*, especially distally; rest of venation essentially as in *permanus*.

The hind wing of this insect is apparently represented by a wing (no. 4665) 14 mm. long and 3.9 mm. wide; its shape is like that of the specimen just described, except that the anal margin is more broadly rounded.

Holotype: No. 4666ab, Museum of Comparative Zoology; collected in Midco insect bed (loc. 8-M), Noble Co., Oklahoma (F. M. Carpenter & G. O. Raasch). This is a complete and splendidly preserved wing. Paratype: No. 4665ab, Museum of Comparative Zoology; same collecting data; it is a complete wing with a more broadly rounded anal margin than the holotype, but with an identical venation, except for the position of the cross-veins.

In addition to these specimens there are two others, not so well preserved; no. 4686ab (loc. 15-L),

a hind (?) wing; and no. 4683 (loc. 12-M), a fore (?) wing.

Although the wing of *curvatus* resembles that of *permanus* in general form, it differs chiefly in having the posterior margin curved for its entire length, and in having a more sharply pointed apex. The wing membrane of *curvatus* is curiously uneven. The occurrence of this peculiarity in all specimens of *curvatus* shows that it is not an individual condition or the result of unusual preservation. Viewed under oblique light the membrane forms a series of shallow bulges and depressions. No other protohymenid possesses this characteristic, except the following new species (*latus*).

***Protohymen latus*, new species**

Figure 14

Hind (?) wing: length, 15 mm.; width, 4.2 mm.; wing membrane uneven, as in *curvatus*; shape of wing much like that of *curvatus*, but anal margin more broadly rounded; costal margin nearly straight for most part, but starting to curve somewhat before the beginning of the pterostigma; apex slightly more rounded than in *curvatus*; posterior margin curved for its entire length; Sc and R1 as in *permanus*; MA anastomosed with Rs for a very short interval; IA very remote from posterior margin, especially distally; a cross-vein present between IA and margin near base of wing, and one at about the

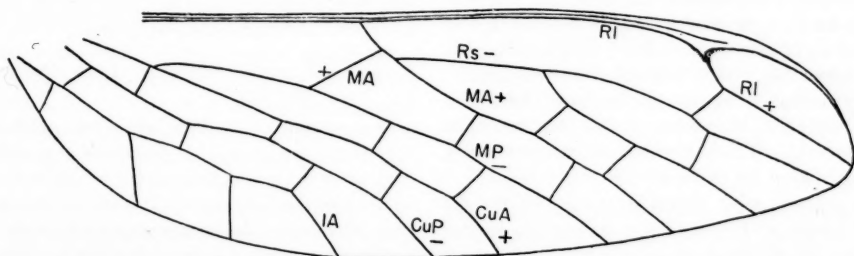


FIGURE 14. *Protohymen latus*, n. sp. Drawing of holotype. Lettering as in figure 1.

same level between CuP and 1A. Rest of venation as in *permanus*.

Holotype: No. 4667, Museum of Comparative Zoology, collected in Midco insect bed (loc. 8-M), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This is a well preserved wing, complete except for the very base of the costal margin. The broadly rounded posterior margin suggests that it is a hind wing and it may eventually turn out to belong to *curvatus*. Both *curvatus* and *latus* have 1A more remote from the margin than it is in any other *Protohymen*; but in *latus* the distance between that vein and the margin is so much greater than in *curvatus* that I believe *latus* to be a distinct insect. The remoteness of 1A from the margin is interesting phylogenetically because it approaches the structure of certain Carboniferous Megasecoptera. The proximal cross-veins between 1A and the margin and CuP and 1A may be individual traits only, but I have not seen them in other specimens of the genus.

***Protohymen venustus*, new species**

Figure 15

Fore (?) wing: length, as preserved. 11 mm.; estimated length of complete wing, 12.5 mm.;

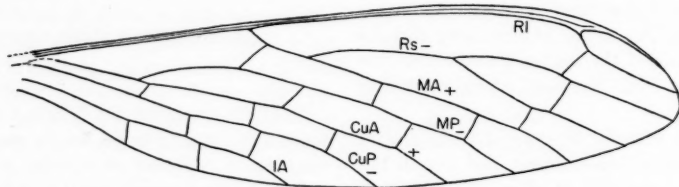


FIGURE 15. *Protohymen venustus*, n. sp. Drawing of holotype. Lettering as in figure 1.

width, 2.8 mm. Membrane smooth, as in *permanus*; slenderly oval in shape; costal margin straight only to the proximal end of the pterostigma, the apical curvature beginning at this point; apex acute; posterior margin regularly curved for its entire length; Sc and R1 as in *permanus*; pterostigma not so broad as in *permanus* and *curvatus*; MA coalesced with Rs for a longer interval than in *curvatus*; rest of venation as in *permanus*. Hind wing unknown.

Holotype: No. 4668, Museum of Comparative Zoology; collected in the Midco insect beds (loc. 15-L), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This is a splendidly preserved wing, complete except for the very base.

This graceful wing differs from that of the described species of *Protohymen* in having the apex of the wing nearly symmetrically curved. In other respects the shape of the wing is more like that of

*curvatus* than of *permanus*, but it is narrower proximally and the membrane is decidedly smooth, as in *permanus*.

***Protohymen largus*, new species**

Figure 16

Fore wing: length as preserved, 18.5 mm.; estimated complete length, 21.5 mm.; width, 4.8 mm.; membrane smooth; costal margin straight as far as the beginning of the pterostigma, the apical curvature beginning at that point; apex nearly symmetrical; middle part of posterior margin straight; Sc and R1 as in *permanus*; pterostigma narrower than in *permanus* and *curvatus*; MA anastomosing with Rs for a very short distance; 1A close to hind margin, as in *elongatus* Carp.; rest of venation as in *permanus*. Hind wing unknown.

Holotype: No. 4671, Museum of Comparative Zoology; collected in the Midco insect beds (loc. 15-L), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). There is a second, more poorly preserved specimen in the collection, no. 4672ab (loc. 12-U); it has a wing length of 15 mm. and a width 13.5 mm.

This is the largest species of *Protohymen* known;

its wing expanse was obviously about 45 mm., whereas that of *permanus* was not over 30 mm. In size and shape the wing approaches that of *elongatus* Carp., from Elmo limestone, but the latter has a pointed and very asymmetrically curved apex, whereas that of *largus* is rounded and nearly symmetrical.

***Protohymen readi* Carp.**

*Protohymen readi* Carpenter, 1933, Proc. Amer. Acad. 68: 425.

One specimen (no. 4679) which appears to be this species is also included in the Oklahoma collection. The wing is 15 mm. long and 3.5 mm. wide and it lacks only the very base. It has the strong cross-vein proximal to the pterostigma as in *readi*, as well as the very pointed apex of the latter. This is the only species of the family Protohymenidae in the col-



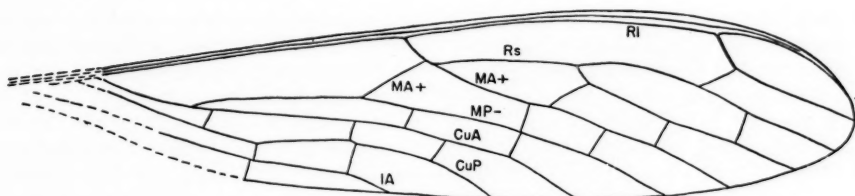


FIGURE 16. *Protohymen largus*, n. sp. Drawing of fore wing (holotype). Lettering as in figure 1.

lection at hand which appears to be common to the Elmo and Midco insect beds.

#### FAMILY ASTHENOHYMENIDAE

These are the most abundant of the Megasecoptera in the Midco beds, so far as the number of individuals is concerned. Slightly more than a hundred specimens are included in the present collection. All of these belong to *Asthenohymen*, the only genus of the family known. A careful study of this material, during which drawings were made of about a third of the specimens, shows that four new species are included, in addition to *A. dunbari* Till. and *A. pusillus* Till., both originally described from the Elmo beds in Kansas. Because of the uniformity of the venation in this genus, the species have been based almost entirely on the shape and size of the wings. It is of course probable that each of these species actually consists of several species, differing from each other in details of body structure, such as genitalia; but we are obviously unable to make such distinctions in the fossils.

Three of the new species described below are unfortunately known only by isolated wings. Presumably, however, the fore and hind wings of these species differ from each other in much the same way as those of *dunbari* and *apicalis*, n. sp., of which complete specimens are known, i. e., the anal margin of the hind wing is slightly more broadly rounded than that of the fore wing and the costal space is somewhat narrower.

Study of the new *Asthenohymenidae* has convinced me that my previous interpretation of the structure of the radial sector requires modification. In my original account of the venation of these insects (1930), I was led to conclude, by analogy with the *Protohymenidae*, that MA was coalesced with Rs much as in the latter, except that the free piece of MA had become transversely arranged, more or less at a right angle to Rs, so as to resemble a cross-vein. This interpretation seemed certain to be correct in view of the condition in the *Protohymenidae*, which were generally considered very closely related

to the *Asthenohymenidae*, and it was accepted by Martynov, Tillyard, and other students of fossil insects. I now believe that, although MA is certainly anastomosed with Rs, the transverse vein mentioned is not part of MA. A comparison of the figures of the *Martynoviidae* (Figure 17), especially *Phaneroneura*, with those of *Asthenohymen*, will make clear my present interpretation of the latter. There is a striking resemblance between the venation of *Phaneroneura* and that of the *Asthenohymenidae*; and the differences are in all cases due to specialization on the part of *Asthenohymen*, except for the number of cross-veins. The most significant feature of the *Martynoviidae* is the nature of the anastomosis between Rs and MA. In *M. longipennis*, the amount of coalescence is very slight—in fact MA hardly more than touches Rs. In *Eu. raaschi*, MA joins R well before the origin of Rs; and in *Phaneroneura* Rs joins R much nearer the base of the wing. In view of the similarity between the venation of *Asthenohymen* and *Phaneroneura*, it now seems to me that the condition in the latter represents a stage through which the *asthenomenid* wing has passed. Hence, the real base of MA in *Asthenohymen* has been completely lost by the proximal migration of its origin; and the transverse vein which has previously been thought to be part of MA is really only a cross-vein. In this connection it is noteworthy that in many specimens of *Asthenohymen* the cross-vein indicated is distal of the point of separation of MA from Rs (see Carpenter, 1930, fig. 4). It is of course true that the number of cross-veins in *Phaneroneura* is not quite so large as in *Asthenohymen*; but it is extremely improbable anyway that *Phaneroneura* itself gave rise to the *Asthenohymenidae*; in all probability a related genus, with a similar structure of Rs and with more cross-veins, was in the direct line of ancestry.

It follows from the foregoing discussion, of course, that the *Asthenohymenidae* are not at all closely related to the *Protohymenidae*. This is of interest because it substantiates the evidence provided by the position of the wings at rest in the two families.

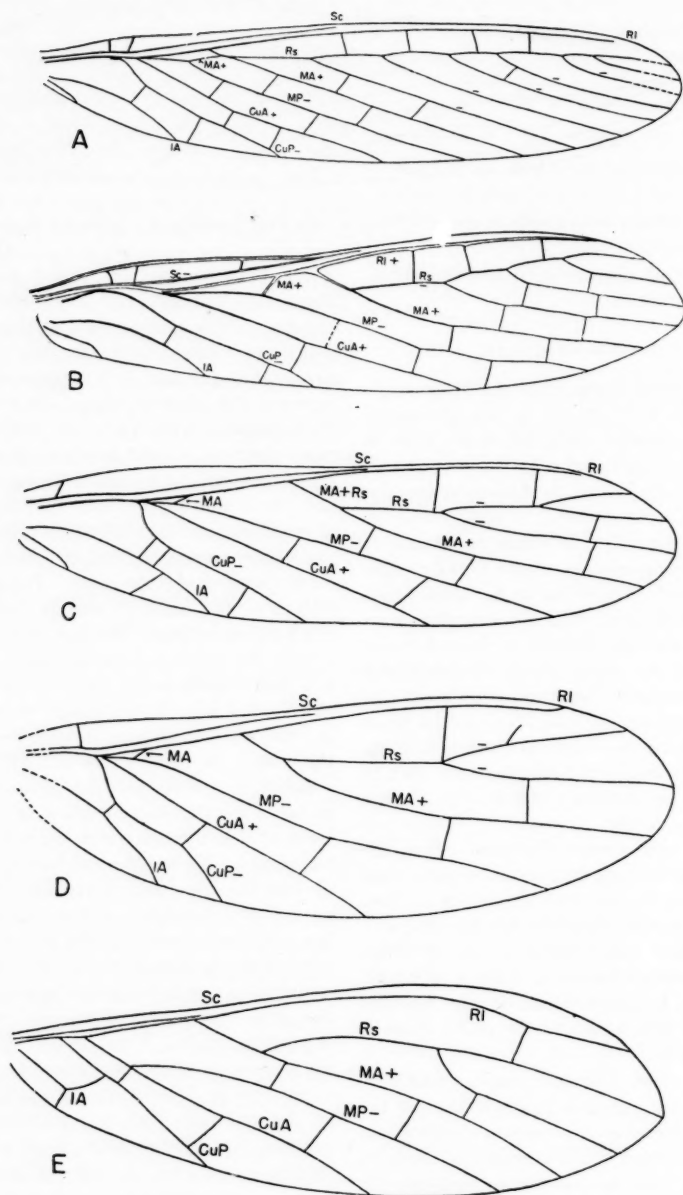


FIGURE 17. Comparison of venation of Martynoviidae and Asthenohymenidae. A, *Martynovia longipennis*, n. sp. (Martynoviidae); B, *Eumartynovia raaschi*, n. sp. (Martynoviidae); C, *Phaneroneura martynovae*, n. sp. (Martynoviidae); D, *Phaneroneura reducta*, n. sp. (Martynoviidae); E, *Asthenohymen apicalis*, n. sp. (Asthenohymenidae). Lettering as in figure 1.



The Asthenohymenidae are known to have been able to fold their wings back over the abdomen at rest, whereas the Protohymenidae were apparently not able to do so. I have discussed this question in my account of the Carboniferous Prochoropteridae (1940), which were also able to fold their wings over the abdomen, and have pointed out there that although at first glance the Asthenohymenidae did not seem at all closely related to the Prochoropteridae, the ability to fold the wings probably did not arise independently in the two families. According to the new interpretation of the asthenohymenid venation, however, the Prochoropteridae and Asthenohymenidae are really very close relatives.

Genus *Asthenohymen* Till.

*Asthenohymen* Tillyard, 1924, Amer. Jour. Sci. 8: 117; Carpenter, 1939, Proc. Amer. Acad. Arts Sci. 73: 31.

***Asthenohymen triangularis*, new species**

Figure 18

Fore wing: length, 10 mm.; width, 3 mm. Proximal part of wing much narrower than the distal part,

The wings of this species are more nearly triangular in shape than those of *dunbari* or *pusillus*. The width of the wing at the level of the origin of CuA is 1.2 mm., whereas the maximum width is 3 mm., or 2.5 times the basal width. The size of the holotype is greater by about 2 mm. than that of any *dunbari* which I have seen from either the Elmo or Midco beds.

***Asthenohymen apicalis*, new species**

Figure 19

Fore wing: length, 7.5 mm.; width, 2.5 mm. Proximal part of wing only moderately wider than the basal part; costal margin very nearly straight, with only a slight bulge at the level of the origin of CuP; apex distinctly pointed, the apical curvature beginning before the level of the pterostigmal cross-vein; posterior margin at least slightly curved for its entire length; R1 slightly curved away from margin at pterostigma; pterostigma distinctly darker than the rest of the membrane; 2A short, as in *triangularis*; venation in other respects like that of *dunbari*.

Hind wing: similar to fore wing in size, venation

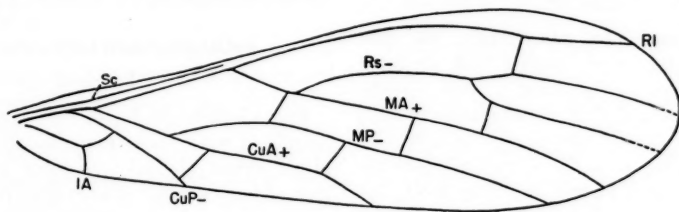


FIGURE 18. *Asthenohymen triangularis*, n. sp. Drawing of fore wing (holotype). Lettering as in figure 1.

the wing as a whole being narrowly triangular; costal margin very nearly straight, with a slight bulge above the origin of CuP; apex rounded, the apical curvature beginning at about the pterostigmal cross-vein; posterior margin nearly straight at the middle part; R1 slightly curved away from margin at pterostigma; pterostigma not perceptibly pigmented in type; 2A short, as in *pusillus*; venation in other respects like that of *dunbari*.

Holotype: no. 4717, Museum of Comparative Zoology; collected in the Midco insect beds (loc. 15-L), Noble Co., Oklahoma (F. M. Carpenter and R. O. Raasch). This specimen consists of a complete and splendidly preserved wing; its narrowed anal region indicates that it is a fore wing. In addition to the type there are two other specimens (nos. 4716, 4743) which have a wing-shape like that of the holotype, but the length of the wings is only 6 mm.

and shape (including pointed apex), but anal region is slightly broader.

Holotype: no. 4722, Museum of Comparative Zoology; collected in Midco insect beds (loc. 15-L), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This consists of a splendidly preserved and complete fore wing; no. 4700 (loc. 15-L), a complete fore wing; no. 4705 (loc. 31), a complete fore wing; no. 4710, a complete hind wing; no. 4721 (loc. 15-L), a complete hind wing; No. 4744 (loc. 15-L), a nearly complete fore wing; no. 4745 (loc. 4-L), a complete fore wing; no. 4783 (loc. 8-M), a complete specimen, with parts of all wings, thorax and abdomen; the body is 12 mm. long, which is about one and a half times the length of *dunbari*. The eyes seem more protuberant than in *dunbari*, though preservation may be the cause of this difference.

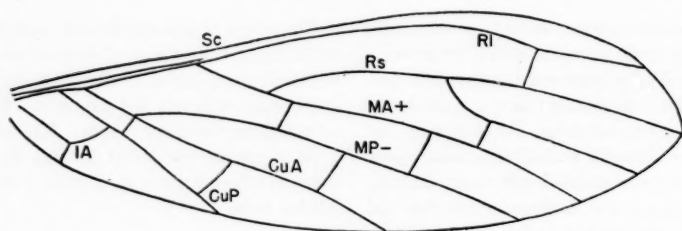


FIGURE 19. *Asthenohymen apicalis*, n. sp. Drawing of fore wing, based mainly on holotype. Lettering as in figure 1.

This species is distinguished from *dunbari* and other described members of the genus by the pointed apex and strongly curved posterior margin. It is the commonest species of *Asthenohymen* in the Mideo beds, next to *dunbari*, there being ten other specimens (nos. 4746 or 4727) in the collection in addition to the types. I have identified specimens nos. 4721 and 4710 as the hind wings of this insect because they differ from the holotype just as the fore and hind wings of *dunbari* differ.

***Asthenohymen parvulus*, new species**

Figure 20

Fore wing: length, 4.3 mm.; width, 15. mm. Distal part of wing much broader than proximal part; costal margin nearly straight, with a slight bulge over the origin of CuP; distal margin of wing broadly curved, but the very apex is pointed; R1 curved away slightly from the margin at pterostigma; 2A close to hind margin and very short, the curved cross-vein joining it to 1A being fully as long as the part of 2A from the cross-vein to the base; venation in other respects as in *dunbari*.

Hind wing: a specimen which I have identified as the hind wing of this species is 4.2 mm. long and 1.5 mm. wide and has more or less rounded anal margin; in other respects it is similar to the fore wing.

Holotype: No. 4747, Museum of Comparative Zoology; collected in the Mideo beds (loc. 15-L), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This specimen is a remarkably well pre-

served and complete fore wing. Paratypes: No. 4698 (loc. 15-L); this is a complete hind wing, well preserved; No. 4711 (loc. 15-L), a complete fore wing having the same size, shape and venation as the holotype.

This insect, which could not have had a wing expanse of more than 10 mm., is the smallest Megasecopter known. The wings are shaped somewhat like those of *triangularis*, but are less than one-half as long and of course have a pointed apex. The narrowed anal area of the fore wing has brought 2A closer to the wing margin than in other known species of the genus.

***Asthenohymen latus*, new species**

Figure 21

Fore wing: length 7 mm., width 2.2 mm. Costal margin of wing nearly straight, only a slight bulge above origin of CuP; posterior margin strongly curved for its whole length; apex rounded, but the very tip pointed; wing broadest just beyond middle; R1 strongly curved away from margin at pterostigma; pterostigma strongly pigmented in holotype; Cu2 extremely short, the cross-vein connecting it to 1A being closer to the base of CuA than in other species. Hind wing: similar to the fore wing, but with slightly more rounded anal margin; the specimen identified as a hind wing has a length of 7 mm. and width, 2.5 mm.

Holotype: no. 4720, Museum of Comparative Zoology; collected in Mideo insect beds (loc. 15-L),

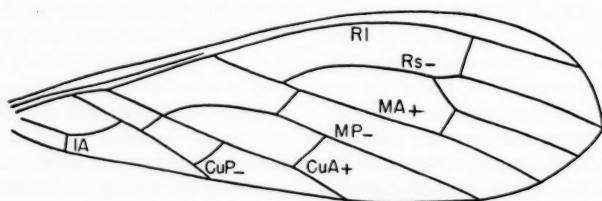


FIGURE 20. *Asthenohymen parvulus*, n. sp. Drawing of fore wing (holotype). Lettering as in figure 1.

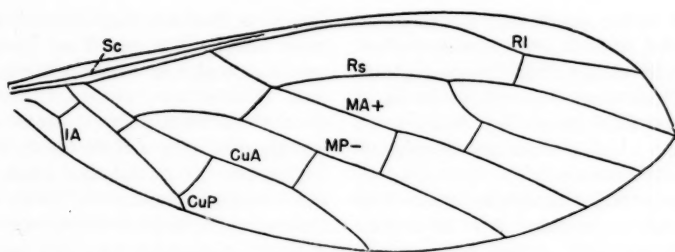


FIGURE 21. *Asthenohymen latus*, n. sp. Drawing of fore wing (holotype). Lettering as in figure 1.

Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This is a very well preserved and complete fore wing. Paratypes: no. 4702 (loc. 15-L), a complete fore wing; no. 4782 (loc. 8-M), a complete hind wing.

This species resembles *apicalis* in having the strongly curved posterior margin, but the extreme width of the wing is unique, as is also the basal part of the cross-vein between 1A and 2A.

*Asthenohymen dunbari* Till.

*Asthenohymen dunbari* Tillyard, 1924, Amer. Jour. Sci. 8: 117; Carpenter, 1939, Proc. Amer. Acad. Arts Sci. 73: 31.

In the Midco collection there are about forty well preserved specimens which appear to be identical with *dunbari*, originally found in the Elmo limestone. All of these specimens consist of isolated wings and it is of course possible that the Oklahoma specimens differed from those in the Elmo limestone in body structure (e. g. genitalia); but until evidence to the contrary has been found, I consider them to be *dunbari*.

*Asthenohymen pusillus* Till.

*Asthenohymen pusillus* Tillyard, 1926, Amer. Jour. Sci. 11: 68; Carpenter, 1933, Proc. Amer. Acad. Arts Sci. 68: 429.

Seven specimens of this insect are present in the Oklahoma collection. As I have pointed out in the case of *dunbari*, we have no way of knowing whether or not the body structure differed from that of the Kansas material. It is interesting to note that *pusillus* is rarer than *dunbari* in both the Elmo and Midco beds.

THE VENATION AND RELATIONSHIPS  
OF THE MEGASECOPTERA

The term "Megasecopterida" was first used by Brongniart (1885) for a "family" of several genera from the Carboniferous of France and England. This group he originally (1885) placed in his Order Pseudo-Neuroptera, together with the Protodonata

and Protphemmerina; but later (1894) he assigned it to the "Neuropteroid series" of the Order Palaeodictyoptera. Handlirsch subsequently (1906) elevated the Megasecopterida to an order, changing the name to Megasecoptera. Additional Carboniferous genera, including four from North American deposits, have been referred to the order by Seudder, Handlirsch, Meunier, and Carpenter. The first Permian Megasecoptera (*Prothymen*, *Permohymen* and *Asthenohymen*) were found in Kansas and described by Tillyard (1926) in a new order, Protohymenoptera, considered by him ancestral to the Hymenoptera. Other representatives of this group, subsequently collected in the Kansan and Russian Permian, furnished evidence that the Protohymenoptera were really closely related to the Megasecoptera and could be considered a suborder within it. During the past twenty years sixteen more genera of Permian Megasecoptera have been described, some being obviously allied to the Protohymenoptera, and others to the Carboniferous or Eumegasecopterous families. It has now become apparent that the Order Megasecoptera, instead of being primarily a Carboniferous order, did not attain its maximum development until the Permian Period. The interrelationships of these Permian and Carboniferous genera have not been at all clear, and the whole picture of the order has been most confused; but some of the recently discovered fossils, including those described above, have indicated what appears to be the general pattern of evolution within the order, and, at the same time, have raised broader questions of the relationships between the Megasecoptera and other orders.

When, in 1926, Tillyard described the so-called Protohymenoptera from the Kansan Permian, he noted that although the Protohymenidae (*Prothymen* and *Permohymen*) were always preserved with their wings outspread, i. e., in the usual palaeopterous condition, the *Asthenohymenidae* were preserved with their wings folded over the abdomen, i. e. in the usual neopterous condition. He later

(1936) elaborated on the significance of this difference, and concluded that, "It must now be evident that a group of insects, the Order Megasecoptera, which began as Palaeoptera, have within the limits of a single small derived group, the Protohymenoptera, evolved into a highly specialized Neopterous type, the family Asthenohymenidae! I do not suppose that anybody will attempt to claim that *Asthenohymen* should be separated from its obvious relatives, *Protohymen* and *Permohymen*, which rested with their wings outspread, in order to preserve the two subdivisions Palaeoptera and Neoptera, which are now seen to cut across the actual phylogeny of these ancient groups. The only logical course is to suppress the two groups Palaeoptera and Neoptera, and adopt a classification more in keeping with the facts.

"Surely it must have been obvious for a long time that all Neoptera have been derived from extinct Palaeopterous types. Now the fossil record shows us a group, Protohymenoptera, of either ordinal or subordinal rank, whichever you prefer, in which the change is seen actually taking place . . . My conclusion is that the Order Protohymenoptera shows affinities with both the Megasecoptera and Hymenoptera. It should be regarded as a specialized offshoot from the common ancestor of the Megasecoptera and the Odonatoid complex . . . and, at the same time, as a remnant of the group from which the Hymenoptera have been evolved."

I have quoted these two paragraphs because they were Tillyard's last statements relative to the Protohymenoptera and because of their broad phylogenetic implications. If I understand these remarks correctly, Tillyard contends (1) that the neopterous condition is of polyphyletic origin, and (2) that the Hymenoptera are derived, through the Protohymenoptera, from the common ancestors of the Megasecoptera and the odonatoid complex. It is to be noted that no mention is made of the Neuroptera, Mecoptera, and other holometabolous insects which are usually regarded as close relatives of the Hymenoptera. However, in 1932 (p. 23) Tillyard remarked that if the Protohymenoptera should turn out to be "descended from Megasecoptera, then we may also have to reconsider Handlirsch's view that the Neuroptera are similarly derived."

Since the above articles were written, several fossils have been found which indicate that the origin of the neopterous condition in the Protohymenoptera is not so simple as Tillyard supposed. Tillyard himself subsequently described (1937) another Megasecopteran (*Elmoa*) from the Kansas Permian, representing a new family and in his opinion a rem-

nant of a very old megasecopterous group. This insect subsequently turned out (Carpenter, 1943) to have the neopterous wing condition, like *Asthenohymen*. Furthermore, certain Carboniferous genera are now known to share the same characteristic—two American genera of the family Prochoropteridae (Carpenter, 1943) and the genus *Diaphanoptera*, from France (Brongniart, 1885). Other related families, as the Martynoviidae, were almost certainly similarly neopterous, although, since no complete specimens have been found, we have only indirect evidence of it.

Such a series of forms at once suggests that the ability to fold the wings over the abdomen, instead of being developed independently by the Permian *Asthenohymenidae*, arose in a more ancient and generalized stock. This conviction is strengthened by the obviously close relationship between the groups mentioned. A comparison of the wings of the Elmoidae, Martynoviidae and *Asthenohymenidae* reveals several striking characteristics common to all. The most obvious of these is the proximal convergence of the strongly convex CuA and R, forming an angle bisected by the stem of M; another is the relative remoteness of R1 and Sc from the costal margin, as contrasted with the position of these veins in the Protohymenidae. I have shown above, under the account of the *Asthenohymenidae*, that the venation of this family can best be explained by comparison with that of the Martynoviids, not with that of the Protohymenids. It is therefore my conviction, on the basis of the evidence now at hand, that the families mentioned (*Diaphanopteridae*, *Prochoropteridae*, Elmoidae, Martynoviidae, *Asthenohymenidae*) form a single phylogenetic line, all having the ability to fold their wings over the abdomen when at rest,\* and that the other families, such as the Carboniferous *Aspidothoracidae*, *Corydaloididae*, *Mischopteridae* and the Permian *Protohymenidae*, belong to another phylogenetic line, all holding the wings outspread at rest. This concept separates the family *Asthenohymenidae* from the *Protohymenidae*, and indicates that both of these families are highly specialized members of widely divergent lines. The only other alternative is to assume that the *Asthenohymenidae* have independently developed the neopterous wing folding, the convergent R and CuA, and the other characteristics common to the Elmoid group. Such an assumption seems most unlikely, at best.

\*It is of course possible that some other described families, represented only by fragmentary specimens, are members of this series.



We are now confronted by even broader questions than were proposed by Tillyard. First, can these two divergent lines be considered members of the one order, Megasecoptera? Second, is the asthenohymenid line derived from the neopterous stock which produced all other neopterous insects, or does it represent an independent development of folded wings? At present we do not have nearly enough evidence to enable us to answer these questions, but there are certain points which can be brought out at this time. Although the nature of the wing venation and articulation suggests that the Asthenohymenidae and Protohymenidae are not so closely related as Tillyard supposed, both families, and the lines they represent, do possess certain characteristics in common. The wing membrane was smooth and glassy, and the fore and hind wings were nearly homonomous. Both the Asthenohymenidae and Protohymenidae, as well as all other Megasecoptera in which such structural details are known, had very long and multisegmented cerci. The inclusion of the asthenohymenid and protohymenid lines within one order has, therefore, some evidence to support it, in spite of other evidence against it.

The answer to the first question will largely be determined by the answer to the second. If it can be shown that the ability to fold the wings over the abdomen was independently developed in the asthenohymenid line, then presumably there could be no objection to including both lines in the one order. On the other hand, if it can be shown that all or any other orders of neopterous insects have been derived from the asthenohymenid line, the two lines should probably be separated into different orders. The latter possibility has several interesting and significant implications. Tillyard has expressed the conviction (1926) that the Hymenoptera have been descended from his Order Protohymenoptera and specifically from the protohymenid, rather than the asthenohymenid stock. This clearly means an independent development of the neopterous condition in the Hymenoptera and the Asthenohymenidae, for the protohymenid line was obviously palaeopterous. Tillyard has also suggested that the Neuroptera (and presumably all panorpoid orders) were derived from the Megasecoptera (1932), but he does not indicate whether he had reference to the Protohymenidae or some other group of Megasecoptera. This recalls Handlirsch's proposal that the Mecoptera, Trichoptera, Diptera, and Lepidoptera are descended from the Megasecoptera, though he concluded also that the Neuroptera and Megaloptera were independently evolved from the Palaeodictyoptera, and he postulated a polyphyletic origin of

complete metamorphosis. The latest and most radical suggestion is by Forbes (1943), who contends that all the Megasecoptera, including Protohymenidae, had complete metamorphosis and that the genus *Diaphanoptera* was really a primitive genus of Neuroptera.

I have discussed these phylogenetic questions to show the full significance of some of the suggestions which have been made regarding the relationships of the Megasecoptera. In my opinion, far too little evidence is available to enable us to come to any conclusions on these issues. Furthermore, I consider it futile to make taxonomic changes, such as transferring the genus *Diaphanoptera* to the Neuroptera, until the evidence is more nearly conclusive. It is, of course, highly profitable to consider the possible phylogenetic position and significance of fossil and Recent forms, but to change the systematic position of the genera and families according to the latest piece of evidence serves only to increase confusion.

I do propose, however, a modification of the use of the terms "Protohymenoptera" and "Eumegasecoptera." The former was originally employed by Tillyard as an ordinal name to include the Protohymenidae and Asthenohymenidae; but in more recent years it has been used to include all the Megasecoptera-like forms from Permian strata. "Eumegasecoptera" has been employed as a subordinal name for all Carboniferous Megasecoptera. The separation of the families Asthenohymenidae and Protohymenidae into distinct phylogenetic lines, as suggested above, requires a slight change in the concept of the term Protohymenoptera. Since Tillyard specifically stated that the Protohymenidae were the typical members of the Protohymenoptera, they should presumably be included under the latter; and I propose to place also under the Suborder Protohymenoptera the other families of the protohymenid line mentioned above, i. e., the Aspidothoracidae, Corydaloididae, and Mischopteridae. Similarly, I propose that the members of the Asthenohymenid line (*Diaphanopteridae*, *Prochoropteridae*, *Elmoidae*, *Martynovidae*, and *Asthenohymenidae*) be placed in the Suborder Eumegasecoptera. The position of other megasecopterous families, both Carboniferous and Permian, will not be clear until more of their structure is known.

#### Order PROTODONATA

Seventeen specimens of three species of Protodonata are included in the Mideo Collection. These figures indicate that members of the order are relatively less common in the Mideo than in the Elmo beds, which has yielded thirty-six specimens of six

species. However, the larger size of the entire collection from Elmo is at least partially responsible for the discrepancy in the figures.

The three protodonates from the Midco beds belong to the family Meganeuridae, each to a different subfamily. All the Elmo species are likewise Meganeurids,<sup>7</sup> but whereas most of the specimens from Midco are Meganeurines, the majority of those from Elmo are Typines.

#### Family MEGANEURIDAE

#### Subfamily MEGANEURINAE

#### Genus *Meganeuropsis* Carp.

*Meganeuropsis* Carpenter, 1939, Proc. Amer. Acad. Arts Sci. 73: 39.

This genus was established for a single species (*permiana*) from the Lower Permian of Kansas (Elmo). The species was represented only by two wing fragments of different individuals, but enough was preserved to indicate that the insect was allied to *Meganeura* and that it was at least as large as the Carboniferous *M. monyi* Brongn., from France. In the Midco collection there are thirteen specimens of *Meganeuropsis*, all apparently belonging to one species, described below as *americana*. These additional specimens enable us to form a more satisfactory conception of the genus than previously. In the fore wing, the precostal space is long and tapering, extending beyond the middle of the wing, as in all Meganeuridae. Sc continues very nearly, if not entirely, to the apex of the wing. The stems of R and M are partially fused, forming a double vein, as in other Meganeuridae. Rs arises nearly at the separation of R and MA, at a point slightly along MA. R4 + 5 originates about one-fourth the wing length from the base. At the origin of R2 there is a distinct oblique vein, as in the Typinae. One or two cross-veins between 1A and CuP near the base of the wing are slightly oblique, as in *Meganeura*. The area between 1A and the posterior margin is like that of *Meganeura* though the coriaceous area at the very base is not so extensive. The hind wing is unknown, except for a very small piece at the base, showing a strongly curved CuP, as in *Megatypus*.

*Meganeuropsis* differs from *Meganeura* in having a narrower precostal area basally and a smaller coriaceous area at the base of the anal region. Other differences will probably be apparent when the complete fore wing of *Meganeura* is known. The oblique

vein at the origin of R2 has not been seen in any species of *Meganeura*.

The two known species of *Meganeuropsis* were very large; the new Midco species was about the size of *Meganeura monyi* Brongn. (Commentry, France) while the genotype (*permiana*) was even larger. There is no doubt that *Meganeuropsis* is closer to *Meganeura* than to *Megatypus* and its relatives; but the differences between the Meganeurinae and Typinae are not so great as has been thought. Tillyard (1924, 1925) separated the two subfamilies on the position of origin of R4 + 5 (R3, Tillyard's notation), but the origin of this vein is actually identical in *Meganeura* and *Megatypus* (Carpenter, 1943). The only obvious difference between the two subfamilies is in the length of the precostal area.

#### *Meganeuropsis americana*, n. sp.

Figures 22, 23; plate 1, figure 2.

Fore wing: length, as preserved, 280 mm.; estimated entire length, 305 mm. Maximum width, 50 mm. The wing is slender, especially basally. Details of venation are shown in figure 22. Specific characteristics are difficult to select, but probably in this category are the point of origin of R2 + 3 (just proximal of first posterior veinlet of MA), the position of the origin of R2, and the general nature of all branches.

Holotype: No. 4805ab, Museum of Comparative Zoology (loc. 15-L), a very well preserved fore wing, 260 mm. long and 50 mm. wide; it lacks only the apex and a piece along the posterior border. Paratypes: No. 4812ab (loc. 12-M), consisting of a distal piece of a fore wing, from the origin of R2 + 3 to the apex, 115 mm. long. No. 4806ab (loc. 15-L), a piece of the middle of a fore wing, 95 mm. long and 35 mm. wide. No. 4807ab (loc. 15-L), an apical part of a fore wing, 105 mm. long and 45 mm. wide. In addition there are eleven fragments (not designated types), nos. 4808-4811, 4813-4818, from localities 15-L, 8-M, 12-M. Only one appears to be a hind wing; it consists of a piece of a wing base from Sc to 1A, 45 mm. long with CuP very strongly arched as in the hind wings of other Meganeurids. All specimens were collected in the Midco insect beds, Noble County, Oklahoma, by F. M. Carpenter and G. O. Raasch.

This species is undoubtedly closely related to the genotype (*permiana*), which is, however, known only from two fragments, one being the proximal part of a hind wing. Since the cells are larger and the veins thicker in the fragments of *permiana* than they are in *americana*, the former was probably the larger

<sup>7</sup> The family Calvertiellidae, known only from Elmo, is now placed in the Palaeodictyoptera. See Carpenter, 1943, pp. 536, 548.

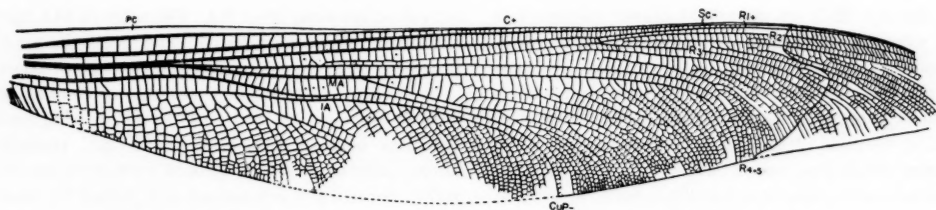


FIGURE 22. *Meganeuropsis americana*, n. sp. Drawing of fore wing, based on holotype and paratypes 4812, 4807. R2, R3 and R4+5, branches of Rs; pc, precostal space; other lettering as in figure 1.

insect. More specimens of *permania* may indicate that *americana* is identical with it, but until that is certain, I believe the two should be considered distinct.

The holotype wing of *americana*, which is 260 mm. long, is, so far as I am aware, the largest continuous specimen of a wing known. All specimens of *Meganeura monyi*, which had about the same wing expanse as *americana*, consist of smaller fragments. Two of the paratype specimens of *americana* (nos. 4812, 4807) show about 40 mm. more of the distal part of the wing than is preserved in the holotype; since the overlapping areas of these two fossils and of the holotype agree remarkably well, I have added the distal part of these paratypes to the holotype in the drawing of *americana*, figure 22. This brings the length of the part of the wing actually preserved to 300 mm., which is about 5 mm. less than the estimated length of the complete wing.

There are three aspects of *americana* which deserve further comment. One of these is the presence of an oblique vein above the point of separation of R2 and R3. This is obviously the homologue of the vein Sn which Sellards described in *Typus permianus* and which also occurs in *Megatypus schucherti* (Carpenter, 1939). We do not yet know that such a vein existed in *Meganeura*, since the area concerned is not well preserved in any specimen, but I presume it did.

The phylogenetic significance of this vein is not clear, though it is probably homologous with Sn of the Odonata.

Another interesting feature of the venation is the thickening of Sc near the point of contact with R1 (Figure 23B). Although only 10 mm. long, it is nevertheless distinct and appears to be an incipient pterostigma, not unlike that of some Megasecoptera (e. g. Protodynemenoptera). No such structure has previously been observed in the Protodonata.

The third noteworthy feature is the presence of plate-like thickenings on the membrane of the wing near the middle of several cells. Their distribution over the wing is indicated in the drawing (Figure 22). Eighteen are clearly discernible in the holotype, and others, not distinct enough for recognition, may also be present. In one of the paratypes (no. 4806) there are a few more platelets than in the holotype, although their general arrangement is the same; and in specimen no. 4817, which is part of a hind wing, there are two between 1A and CuP near the base. Under high magnification they appear to consist of a minute central disc within a larger, less thickened one, about .5 mm. in diameter. Identical structures have been described by Bolton on the wings of the meganeurid *Boltonites radstockensis* (Bolton) from the British Coal Measures, and a few are discernible in the published photograph of this insect (1914, pl.

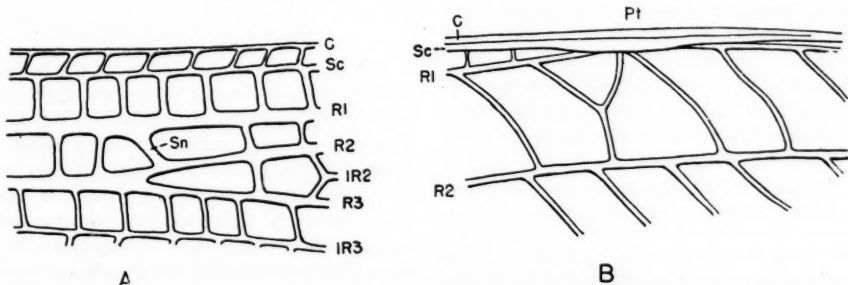


FIGURE 23. *Meganeuropsis americana*, n. sp. A. Drawing of venation in the region of separation of R2 and R3 (holotype). IR2, IR3, intercalary veins; for explanation of Sn, see text. B. Drawing of venation near end of Sc (holotype). Pt, incipient "pterostigma".



18, fig. 1). Reis has described similar markings on the wings of *Reisia gelasii* (Reis), a possible Protodonatan from the Jurassic of Germany. To my knowledge, these are the only recorded occurrences of such platelets on odonatoid wings. However, since noting them in *Meganeuropsis*, I have looked for similar structures, under relatively high power, on Protodonate wings from the Elmo beds, in Kansas. They are very distinct in the specimen of *Megatypus schucherti* which I figured in 1943 (Plate 1, fig. 1)—17 between 1A and CuP and a few others in the anal area. None are discernible in specimens of *Typus* or *Oligotypus*. The precise nature of these structures is not at all clear. They may be setal bases, though in that case we should expect to find at least a few of the setae preserved.<sup>8</sup> Handlirsch has compared those of *Reisia* with similar structures in the Protorthopterous genus *Carcugus* (1911). The latter, however, seem more like the nygmata of various Recent holometabolous insects (see Navas, 1917; Forbes, 1924; Brues, 1933).

#### Subfamily TYPINAE

##### Genus *Typus* Sell.

This genus is represented by two species from the Elmo beds in Kansas, and two from the Permian of Arizona. In the Mideo collection there is another very distinct species.

##### *Typus gracilis*, n. sp.

Figure 24; plate 1, figure 1.

Fore wing: length, 145 mm.; greatest width, 26 mm.; slender. Costal margin straight, apex narrowly rounded, posterior margin with maximum width at level of first fork of MA. The distal half of the posterior margin has a slight arcuate curvature. Only part of the precostal area is preserved; it is similar to that of *permanus*. Sc approaches close to the costal margin at about the level of the origin of R3, but it remains independent of the costa until near the apex of the wing; R1, Rs, and MA arise as in all Typinae; first fork of Rs as in *permanus*, although R2 + 3 and R4 + 5 diverge more gradually; R2 and R3 separate at about two-thirds the wing length from the base; oblique vein (Sn) present as in other Typinae. R2 diverges away from R1 a short distance before the apex of the wing, and IR2 simi-

larly diverges away from R2. Branches of MA more extensive than in *permanus*. The "vestigial CuA" is present as in *permanus*, except that it appears to fork basally. Two slightly oblique cross-veins are present between 1A and CuP near the wing base. Distance between the base of 1A and posterior margin somewhat greater than in *permanus*, and the veins traversing this area are not joined by cross-veins. The cross-veins in the wing as a whole are about as numerous as those in *permanus*, much fewer than in *readi*. Hind wing unknown.

Holotype: no. 4818, Museum of Comparative Zoology; collected in Mideo insect beds (loc. 12-M), Noble Co., Oklahoma, by G. O. Raasch. This specimen consists of a complete and well preserved fore wing (plate 1), and is one of the most striking fossils in the Mideo collection.

This species presumably had a wing expanse of about 300 mm., nearly one and a half times that of *permanus*. It also differs from *permanus* in having a more slender wing and straighter veinlets between 1A and the posterior margin proximally. It differs from *T. readi* in wing shape and especially in having fewer cross-veins (Carpenter, 1939, fig. 7).

One of the most interesting features of this wing is the structure of the "vestigial CuA" at the base of the wing. This vein apparently occurs in all Typinae (and even in Meganeurinae; see Carpenter, 1943, fig. 2), but it is more clearly preserved here than in other specimens of the group which I have seen. It is composed of two thin veins, one just below M and abruptly curved posteriorly, and the other near the base of CuP and straight. Since both MP and CuA are missing in the Typinae (as well as Meganeurinae), it may well be that the anterior element is a vestige of MP and the posterior one a vestige of CuA. At present, however, there is no Protodonatan known in which these veins are intermediate between the fully developed and vestigial conditions.

##### Oligotypinae, new subfamily

This subfamily is established for the genus *Oligotypus*, previously known by the genotype specimen from the Elmo beds, and placed in the subfamily Typinae. A new specimen of this insect in the Mideo collection provides further information which convinces me that the genus should be separated from *Typus* and *Megatypus* at least by subfamily rank. The characteristics of *Oligotypus* for which the subfamily is formed are as follows: in the fore wing, R2 + 3 and R4 + 5 are widely divergent; Sc terminates slightly beyond mid-wing; MA lacks true branches, so that the area occupied by MA distally

<sup>8</sup> Dr. W. T. M. Forbes has called my attention to the occurrence of setae on the wing pads of certain odonate nymphs. It is conceivable that in the Protodonata setal bases might have been carried over from the nymphs to the adults.

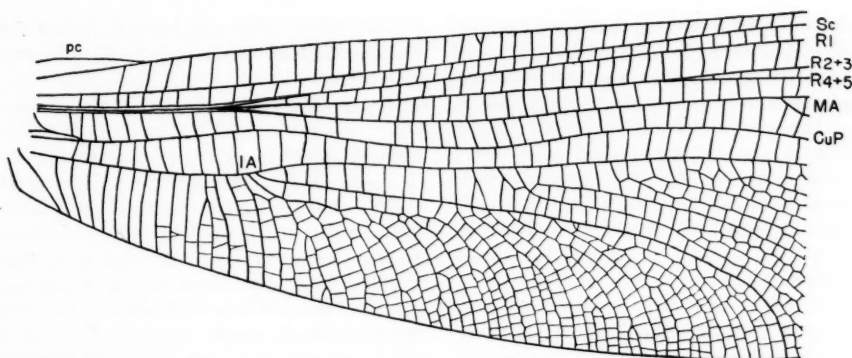


FIGURE 24. *Typus gracilis*, n. sp. Drawing of proximal half of fore wing (holotype). Lettering as in figures 1 and 22.

is very small. The so-called vestigial CuA is completely absent, as is also the oblique vein at separation of R2 and R3. The other two subfamilies of the Meganeuridae (i. e. Meganeurinae and Typinae) are alike in having closely approximate branches of Rs, a longer Sc, a multi-branched MA, and a strong oblique vein at the separation of R2 + R3. *Oligotypus* obviously differs from the Meganeurinae and Typinae more than the latter do from each other. The hind wing of *Oligotypus* is still unknown.

Genus *Oligotypus* Carp.

*Oligotypus tillyardi* Carp.

Figure 25

*Oligotypus tillyardi* Carpenter, 1931, Amer. Journ. Sci. 21: 106.

The specimen (no 4804ab, loc. 15-L) in the Midco collection is a fore wing, and, though lacking the distal quarter, is much better preserved in other respects than the holotype. It is the same size as the holotype (40 mm. long, as preserved, 11 mm. wide) and has a very similar venation; but it includes the proximal part of the wing, which, although I was not aware of it, was absent in the type. The base

of the wing is now seen to be essentially like that of other Meganeurids. The precostal area is small, as in *Typus*, and the wing is decidedly narrow across the base. The most interesting aspect of this part of the wing is the total absence of the so-called vestigial CuA, which is apparently present in all other genera of Meganeuridae. The proximal part of the wing is so very well preserved that I am convinced that its absence is not merely due to lack of preservation.

It should be noted that there is no sign in the new specimen of the "obsolescent MP," which I mentioned and figured in my account of the type of *tillyardi*. Further examination of the type convinces me that the short vein indicated in my drawing (1931, p. 107, fig. 2) is really the stem of M, broken away (by pressure) from the stem of R, with which it is normally contiguous.

#### Order ODONATA

#### Suborder PROTOZYGOTERA

#### Family KENNEDYIDAE

This family is represented in the Midco collection

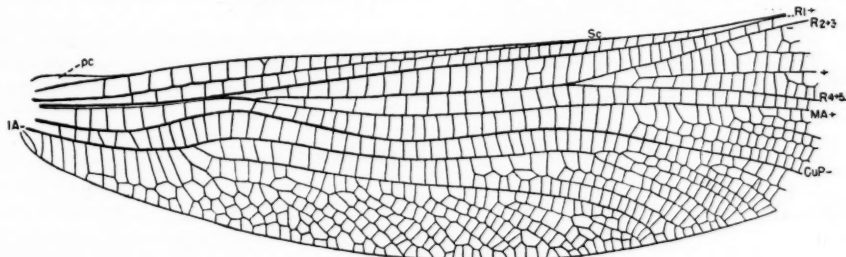


FIGURE 25. *Oligotypus tillyardi* Carp. Drawing of specimen 4804ab, Midco Insect Bed, Noble Co., Oklahoma. Lettering as in figures 1 and 22.

by fifteen specimens, four more than have been secured in the Elmo beds (Kansas). The new fossils belong to the Elmo genera *Progoneura* and *Kennedy*, but include three new species, two of which greatly extend our knowledge of *Progoneura*. The family Kennedyidae has so far been found only in the Wellington formation. The obscure genus *Sushkinia* from the Russian Permian, though originally assigned to this family by Martynov (1930), has subsequently been placed in the family Permolestidae (Martynov, 1937).

#### Genus *Kennedy* Till.

*Kennedy* Tillyard, 1925, Amer. Journ. Sci. 10: 63.  
Carpenter, 1939, Proc. Amer. Acad. Arts Sci. 73: 45.

This genus has previously been known by three species from the Elmo beds: *mirabilis* Till., *tillyardi* Carp. and *reducta* Carp., though the last will probably turn out to belong to another genus. In the Midco collection there is one new species, as well as *mirabilis*. The wings of *Kennedy* are decidedly petiolate and have a distinct nodal bend on the anterior margin; 1A is long, extending well beyond the level of the nodus. Fraser has pointed out (1939) that in this genus the antenodals are aligned with the subcostal cross-veins below, though this is not always strictly the case, as shown by my figures of *mirabilis* and *tillyardi* (1939, p. 46) and in the figures included here. It is true, however, that they are more nearly aligned in *Kennedy* than in *Progoneura*.

In the present collection there are nine specimens of *Kennedy*, of which five are too incomplete for specific determination.

#### *Kennedy fraseri*, n. sp.

##### Figure 26

Wing: length, 40 mm.; width, 5.8 mm. (holotype); shape much as in *mirabilis*; only three postnodals; pterostigma slightly longer than that of *mirabilis*; 1A close to posterior margin; cross-veins much more numerous distally than in either *mirabilis* or *tillyardi*, forming a distinct reticulation; four cross-veins between R2 and 1R2; five between R3 and 1R2; six

between R3 and 1R3; nine between R3 and R4 + 5. Venation similar to that of *mirabilis* in other respects.

Holotype: no. 4793, Museum of Comparative Zoology; collected in Midco insect beds (loc. 3-M), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). This specimen consists of a complete and well preserved wing. It is probably a fore wing.

Paratypes: no. 4790ab, Museum of Comparative Zoology; same collecting data as holotype, but locality 16. This well preserved wing is 34 mm. long and 5.8 mm. wide; it is a little shorter and relatively broader than the holotype and is therefore almost certainly a hind wing. No. 4821ab, also from locality 16; a nearly complete wing, lacking about 4 mm. of the apex. It has the same dimensions as the previous specimen.

This species is named for Dr. F. C. Fraser, who has greatly advanced our knowledge of Odonate evolution. It differs from the previously described species of *Kennedy* mainly by having more cells in the distal part of the wing. Of particular interest is the presence of four cross-veins between R2 and 1R2; in *mirabilis* there are no cross-veins at all in this area, and in *tillyardi* (so far as known) there is only one. The large number of cells in *fraseri* carries a suggestion of the condition in Permolestidae.

#### *Kennedy mirabilis* Till.

*Kennedy mirabilis* Tillyard, 1925, Amer. Journ. Sci. 10: 66; Carpenter, 1939, Proc. Amer. Acad. Arts Sci. 73: 45.

Two specimens apparently belonging to this species are in the Midco collection (no. 4795, loc. 8-M; no. 4798, loc. 5). Each consists only of the distal half of a wing, so that determination is not certain.

#### Genus *Progoneura* Carp.

*Progoneura* Carpenter, 1931, Amer. Journ. Sci. 21: 120. 1933, Proc. Amer. Acad. Arts Sci. 68: 418. 1939, *ibid.* 73: 47.

This genus has previously been known only by three specimens of one species (*minuta*) from the Wellington formation in Kansas. Since all of these

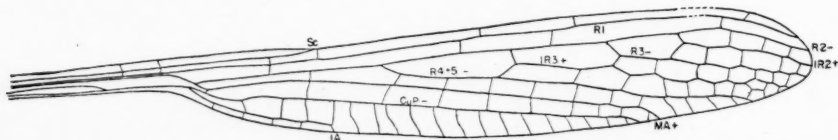


FIGURE 26. *Kennedy fraseri*, n. sp. Drawing of holotype. R2, R3 and R4 + 5, branches of Rs; IR2 and IR3, intercalary branches of Rs; other lettering as in figure 1.

are fragmentary or poorly preserved, little has been known of the wing venation, except the arculus region and the petiole. In the Mideco collection there are five specimens of *Progoneura*, all but one being well preserved and nearly complete wings. It is now possible, therefore, to make a satisfactory comparison of its venation with that of *Kennedyia*.

The wings as a whole, though shaped like those of *Kennedyia*, are not so abruptly petiolate, the proximal half being more tapering. Also, the costal margin is very nearly straight with hardly a discernible break at the nodus. Two or three antenodals are present,<sup>9</sup> not aligned with the subcostal cross-veins below; R1 is very remote from Rs. The stem of the arculus is apparently variable in length; in the genotype it is long but in one of the new species (*venula*) it is very short. CuP + 1A is strongly arched below the stem of arculus, and is more undulated in the petiole than it is in *Kennedyia*. 1A is very short, ending at least at the level of the nodus. Finally, there are only about half as many cross-veins in *Progoneura* as in *Kennedyia*, the venation consequently being very open.

In many respects the genus *Progoneura* is more generalized than other known Protozygoptera. This is indicated by the absence of a nodal bend at the end of Sc, the deviation of the antenodals and the subcostal cross-veins, the tapered petiole, and the undulated CuP + 1A in the petiole. The short 1A and the very small number of cross-veins may also be in this category.

The following species of *Progoneura* are present in the Mideco collection.

***Progoneura nobilis*, n. sp.**

**Figure 27**

Wing: length, 13 mm.; width, 2.5 mm. (holotype). Costal margin with a very slight nodal bend; pterostigma prominent, light reddish brown (as preserved), and slightly swollen; apex pointed; posterior margin conspicuously curved; stem of arculus

<sup>9</sup> The holotype of *Progoneura minuta* (genotype) has a third antenodal between C and Sc just above the arculus, but there is no indication of this in other specimens.

long, 1A terminating below the nodus; R4 + 5 arising at a point far distal to level of nodus; cross-veins arranged as in figure 27. The antenodals and "vestigial CuA" are not preserved, the areas including these structures being broken away.

Holotype: No. 4786ab, Museum of Comparative Zoology, collected in Mideco insect beds (loc. 16), Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). It consists of a complete and well preserved wing.

Paratype: no. 4788ab, Museum of Comparative Zoology, collecting data as for holotype, except for the locality, which is 15-L. This is a nearly complete wing, 15 mm. long and 2.8 mm. wide, lacking only a small piece at the end of MP and at the origin of 1R2. The antenodals are not preserved. The wing is slightly broader at the level of the arculus than it is in the holotype, but the venation is very nearly identical with that of the latter. In all probability the holotype is a fore wing and the paratype a hind wing.

This species is similar in venation to the genotype (*minuta*) but differs in having a much longer arculus stem and in having 1A terminate at about the level of the nodus. Other differences probably exist but further comparison cannot be made because of our incomplete knowledge of *minuta*.

***Progoneura venula*, n. sp.**

**Figure 28**

Wing: length (as preserved), 16 mm.; width, 2.8 mm.; estimated whole length, 17.5 mm. Costal margin without a discernible nodal bend, pterostigma prominent, somewhat longer than that of *nobilis*; apex pointed; posterior margin not so strongly curved as in the latter; stem of arculus very short, much like that in *Kennedyia*, 1A terminating far proximal to the level of the nodus; two antenodals present; the more distal antenodal occurring in *minuta* is not visible in *venula*, possibly because the membrane is partially broken away at the corresponding region. Cross-veins arranged as shown in figure 28.

Holotype: No. 4791, Museum of Comparative Zoology; collected in Mideco insect beds (loc. 16-M),

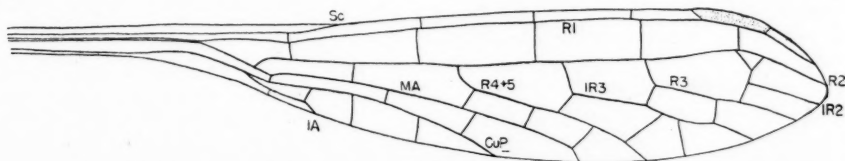


FIGURE 27. *Progoneura nobilis*, n. sp. Drawing of holotype. Lettering as in figures 1 and 26.



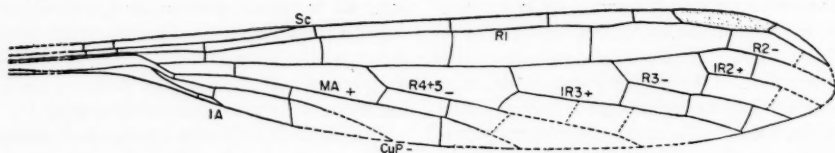


FIGURE 28. *Progoneura venula*, n. sp. Drawing of holotype. Lettering as in figures 1 and 26.

Noble Co., Oklahoma (F. M. Carpenter and G. O. Raasch). The specimen consists of a nearly complete and well preserved wing, lacking the very base of the petiole and a small piece along the posterior margin.

This wing differs from those of *nobilis* and *minuta* in having a very short arculus stem, with the corresponding shift in the position of A1; and in having the origin of R4 + 5 more proximal.

*Progoneura* sp.

In addition to the above, the Midco collection contains one specimen (no. 4792, loc. 8-M), which apparently represents a third species. It consists of the proximal half of a wing, 17 mm. long, indicating that the whole wing was about 34 mm., fully twice the size of other species of the genus. The preserved part of the wing is characteristic of *Progoneura*, but since the nodus and the distal piece of Sc are not known, I believe the species should not be described until more specimens have been found.

Suborder PROTANISOPTERA

Family DITAXINEURIDAE

*Ditaxineura cellulosa* Carp.

*Ditaxineura cellulosa* Carpenter, 1933, Proc. Amer. Acad. Arts Sci. 68: 419.

This species is represented in the Midco collection by the distal fragment of a wing (no. 4801ab, loc. 8-M), 14 mm. long. Its size, venation and pterostigma agree fully with those of *cellulosa*, described from the Elmo beds. The convexities and concavities are very well preserved and show that the posterior "branch" of MA depicted in my figure of *cellulosa* (1933) is really a concave, intercalated sector, as in *anamalostigna*. In the type of *cellulosa* the concavity of the vein was obscured by irregularities.

A second wing fragment (no. 4802ab, loc. 15-L) also belongs to *Ditaxineura*, probably to *cellulosa*, but it consists of the proximal half of the wing only, and is poorly preserved, so that its specific identity is uncertain.

REFERENCES

- BOLTON, H.  
1914. On the occurrence of a giant dragon-fly in the Radstock Coal Measures. Quart. Journ. Geol. Soc., 70: 119-126.
- BRONGNIART, C.  
1885. Les insectes fossiles des terrains primaires. Bull. Soc. Amis. Sci. Nat. Rouen, 1885: 50-68.  
1894. Recherches pour servir à l'histoire des insectes fossiles des temps primaires. Bull. Soc. Industr. Minérale, 7 (4): 124-615.
- BRUES, C. T.  
1933. A new genus of Phoridae from Peru. Psyche, 40 (3): 106-111.
- CARPENTER, F. M.  
1931a. The Lower Permian insects of Kansas. Part 2. The Orders Palaeodictyoptera, Protodonata and Odonata. Amer. Journ. Sci. (5) 21: 97-139.  
1931b. Same, Part 3. The Protelymenoptera. Psyche, 37: 343-374.  
1933. Same, Part 6. Delopteroidea, Protelyptoptera, Plectoptera, and a new collection of Protodonata and Psocoptera. Proc. Amer. Acad. Arts Sci., 68: 411-504.  
1939. Same, Part 8. Additional Megaseoptera, Protodonata, Odonata, Homoptera, Psocoptera, Protelyptoptera, Plectoptera and Protopterlaria. Proc. Amer. Acad. Arts Sci., 73: 29-70.  
1943a. Same, Part 9. The Orders Neuroptera, Raphidioidea, Caloneuroidea and Protorthoptera (Probnisidae), with additional Protodonata and Megaseoptera. Proc. Amer. Acad. Arts Sci., 75 (2): 55-84.  
1943b. Studies on Carboniferous insects from Commeny, France; Part I. Introduction and families Protagriidae, Meganeuridae, and Campylopteridae. Bull. Geol. Soc. Amer., 54: 527-554.
- DUNBAR, C. O.  
1924. Kansas Permian insects. Part I. The geologic occurrence and the environment of the insects. Amer. Journ. Sci., (5) 7: 171-209.
- FORBES, W. T. M.  
1943. The origin of wings and venational types in

- insects. Amer. Midland Natural., **29** (2): 381-405.
- FRASER, F. C.  
1939. A reclassification of the Order Odonata. Austr. Zool., **9** (2)/ 195-221.
- HANDLIRSCH, A.  
1906. Die fossilen Insekten. Wien.  
1911. New Palaeozoic insects from the vicinity of Mazon Creek, Illinois. Amer. Journ. Sci., (4) **31**: 297-326, 353-377.
- MARTYNOV, A. V.  
1930. New Permian insects from Tikhie Gory, Kazan Province. 1. Palaeoptera. Trav. Mus. Geol. Acad. Sci. URSS, **6**: 69-86.  
1937. Permian fossil insects from Kargala and their relationships. Trav. Inst. Paleont. Acad. Sci. URSS, **7**: 1-92.  
1940. Permian fossil insects from Tshekarda. Trav. Inst. Paleont. Acad. Sci. URSS, **11**: 1-62.
- RAYMOND, P. E.  
1944. Late Paleozoic Xiphosurans. Bull. Mus. Comp. Zool., **94** (10): 475-508.  
1946. The genera of fossil Conchostraca—An Order of bivalve Crustacea. Bull. Mus. Comp. Zool., **96** (3): 216-307.
- REIS, O. M.  
1909. Handlirschia Gelasii n. g. et sp. aus dem Schaumkalk Frankens. Abh. K. Bayr. Akad. Wiss., **23** (3): 661-694.
- SARS, G. O.  
1896. Fauna Norvegiæ. Bd. I. Phyllocarida og Phyllopoda. Christiania. Pp. 113-114.
- TILLYARD, R. J.  
1924. Kansas Permian insects. Part 3. The new Order Protohymenoptera. Amer. Journ. Sci., (5) **8**: 111-122.  
1926. Same, Part 6. Addition to the Orders Protohymenoptera and Odonata. Amer. Journ. Sci., (5) **11**: 58-73.  
1932. Same, Part 14. The Order Neuroptera. Amer. Journ. Sci., (5) **23**: 1-30.  
1936. Same, Part 16. The Order Plecoptera (cont'd): The family Doteridae, with a note on the affinities of the Order Protohymenoptera. Amer. Journ. Sci., (5) **32**: 435-453.  
1937. Same, Part 17. The Order Megasecoptera and additions to the Palaeodictyoptera, Odonata, Protoperlaria, Copeognatha, and Neuroptera. Amer. Journ. Sci., (5) **33**: 81-110.
- ZALESKY, G.  
1937a. Nouveaux représentants des Protohymenoptères et des Archodonates provenant du terrain Permien du bassin de la rivière Karna et leurs liens de parenté. Ann. Soc. ent. France, **106**: 101-114.  
1937b. Études des insectes Permien du bassin de la Sylva et problèmes de l'évolution dans la classe des insectes. Prob. Paleont., **2-3**: 601-607.

Harvard University  
Cambridge, Mass.

## EXPLANATION OF PLATES

## PLATE 1

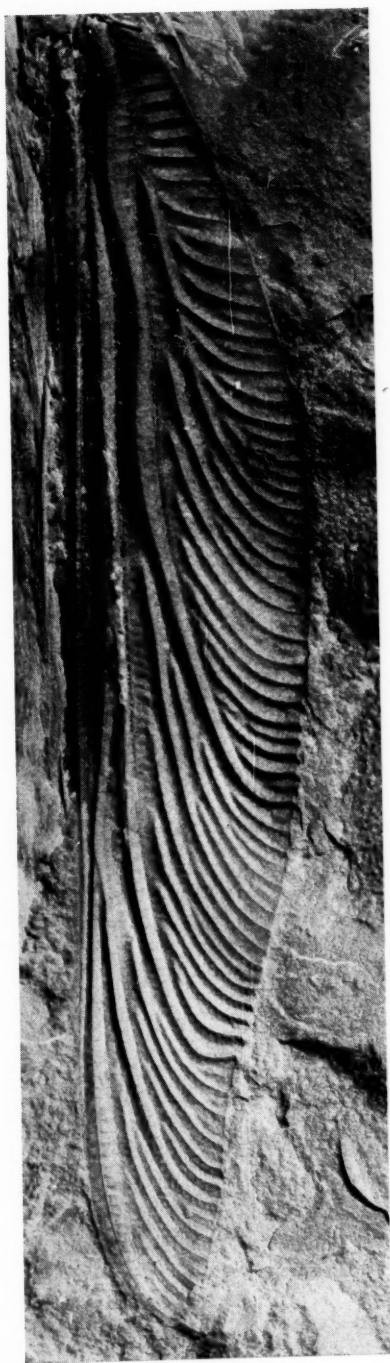
- FIGURE 1. *Typus gracilis*, n. sp. Photograph of holotype (4818).  $\times 1.3$   
FIGURE 2. *Meganeuropsis americana*, n. sp. Photograph of holotype (4805).  $\times .65$

## PLATE 2

- FIGURE 1. *Eumartynovia raaschi*, n. sp. Photograph of holotype (4822).  $\times 8.5$   
FIGURE 2. *Parelmoea revelata*, n. sp. Photograph of holotype (4680).  $\times 12$



PLATE 1



1



2

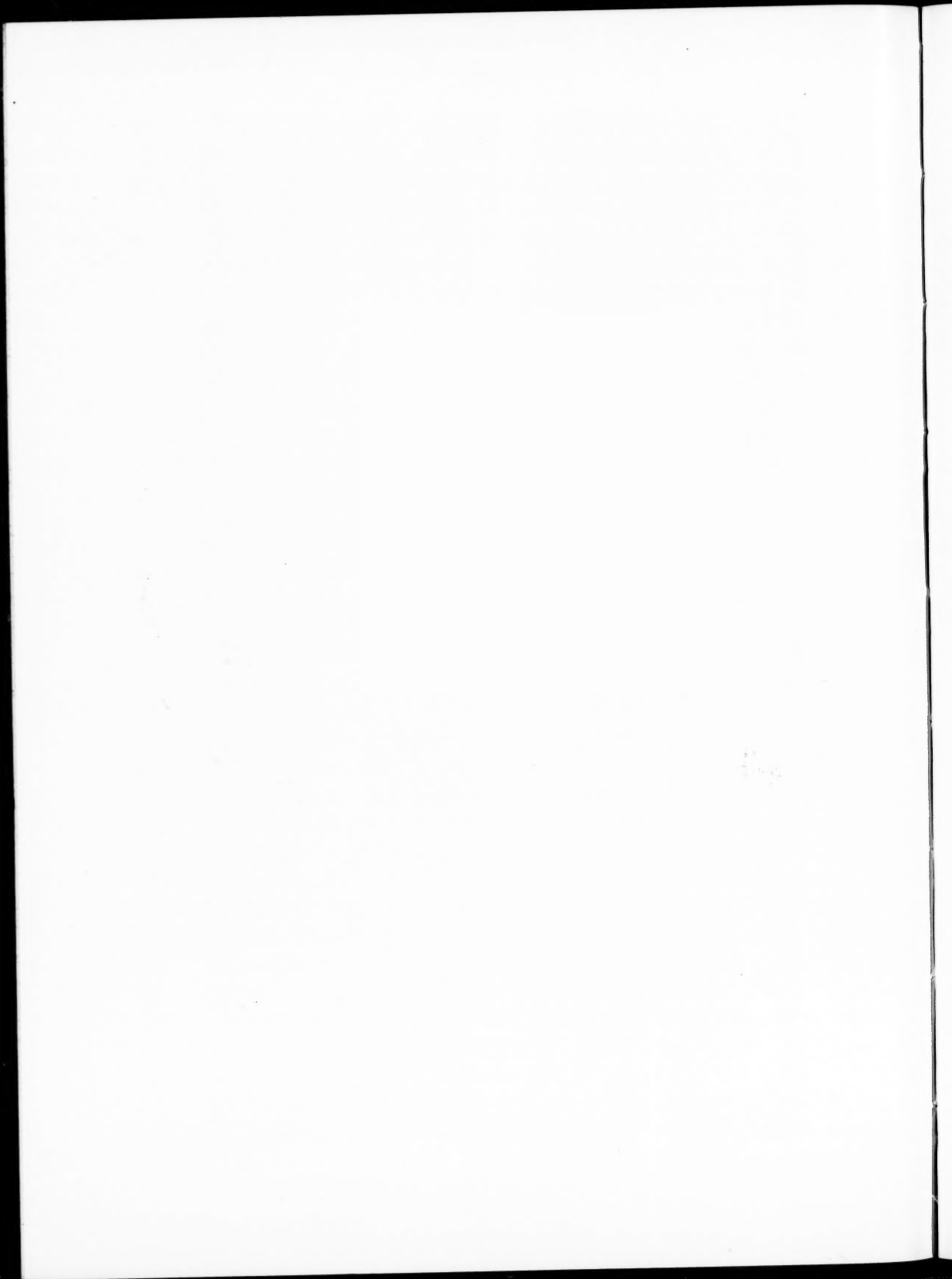


PLATE 2



1



2

